University of Kansas Publications

MUSEUM OF NATURAL HISTORY

VOLUME 10 · 1956-1960

Museum of Natural History
UNIVERSITY OF KANSAS
LAWRENCE
1960

Museum of Natural History

UNIVERSITY OF KANSAS

LAWRENCE

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1960

28-4058

Volume 10

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UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Volume 10, No. 1, pp. 1-44, 6 figures in text, 2 tables
Published September 12, 1956

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED BY
FERD VOILAND, JR., STATE PRINTER
TOPEKA, KANSAS
1956
26-3856

Studies of Birds Killed in Nocturnal Migration

BY

HARRISON B. TORDOFF AND ROBERT M. MENGEL

Contents

Introduction

This paper is primarily an analysis of a sample of migrant birds killed in the autumn of 1954 by striking a television tower one mile west of Topeka, Shawnee County, Kansas. Secondarily, some aspects of migration involved in studies of this kind are discussed and historical background is presented.

Considerable interest has been occasioned in recent years in the eastern United States by large-scale accidents to night-migrating birds. Most accidents have occurred in the autumn. The widespread adoption by airports of an instrument called the ceilometer, which measures the height of cloud ceilings by reflecting from them a high-powered beam of light, has proved under certain conditions to be catastrophic to night-flying birds. Among the recent reports of such accidents are those of Spofford (1949) and Laskey (1951) for Nashville, Tennessee, Howell and Tanner (1951) for Knoxville, Tennessee, and Lovell (1952) for Louisville, Kentucky. Recently Howell, Laskey, and Tanner (1954) reviewed ceilometer "tragedies" without being able to determine the exact reason for their lethal effectiveness. Less publicized so far have been mass collisions of birds with another class of obstacles, tall radio and television towers. These slender towers, usually 500 to 1000 feet tall, are increasing rapidly in numbers and there is reason to suppose that they will take a correspondingly larger toll of bird life.

Notice has long been given by ornithologists to mass destruction of birds by more conventional solid obstructions to passage, and newspapers occasionally mention birds killed at such well-known points as the Washington Monument and the Empire State Building.

Seventy-five years ago, J. A. Allen (1880) published the results of questionnaires circulated by William Brewster to lighthouse keepers. Brewster himself (1886) described destruction of birds at a lighthouse in the Bay of Fundy, paying keen attention to behavior of the birds and the exact conditions under which nocturnal flight and accidents occurred. The subject also received attention in several countries across the Atlantic. Destruction of birds at Irish lighthouses was carefully noted over a period of years and the results were published periodically, culminating in R. M. Barrington's massive report (1900) which remains in some ways the most thorough of its type.

While conservation-minded individuals have been concerned with the tremendous mortality involved in these various events, the ill wind blows some good in that, properly used, the data provided by such accidents can shed light on many obscure aspects of bird migration. Each accidental kill of birds affords a cross-section, approaching in variable degree a random sample, of the migrants passing a given point on a given date. The types of information provided by such kills are numerous, for example: (1) information on the presence of various species and the dates of their occurrence; (2) information on the relative abundance of species; (3) quantitative data on the relative sizes of males and females, and immatures and adults (of importance to taxonomic ornithology); (4) information on the relative times of migration of males, females, adults, and young; (5) information on molts and plumages; (6) quantitative information on composition by subspecies of migrants of the same species; (7) physiological data (fat condition, *etc.*) pertinent to the study of migration; and probably others.

In spite of the great potential of this kind of material, the majority of ornithologists with access to such data have contented themselves with listing the species and sometimes the numbers of birds killed. A few have gone further. James T. Tanner (unpublished) attempted to compute the longevity of the Ovenbird (*Seiurus aurocapillus*) by analysis of ceilometer-killed birds at Knoxville, Tennessee (see below). Mention should be made of the reports of Rintoul and Baxter (1914) supplemented by Ticehurst (1916) who used rather small numbers of birds killed at Scottish lighthouses in studies of molt. However, the only effort to utilize the results of accidental kills on a large scale over a period of years appears to have been that, already mentioned, of Barrington (1900) and his co-workers in Ireland. An idea of the potentialities of the large recent kills in the United States may be obtained when it is recalled that in the 18 years of Barrington's work, which embodied some 1000 reports from lighthouse keepers, Barrington obtained for study only about 2000 specimens, many of these consisting of wings and feet only (Barrington's paper not seen in original; see J. A. Allen, 1901:205). More recently Dobben and Bruyns (1939) have analyzed the age and sex classes of some birds killed at lighthouses in Holland.

As far as we have learned, there is no previous thorough analysis in the literature of large, accidentally-killed samples of birds. On the following pages we emphasize some of the uses which can be made of such material. We think that intensive analyses of such events, whenever they occur, should become a regular part of ornithological investigation and that integration of numerous studies of such incidents will provide an unprecedented mass of information on migration.

Accidents to Migrating Birds in early October, 1954

GENERAL.—The few days around the end of the first week of October, 1954, were notable for a series of accidents which occurred to migrating birds over much of eastern United States. So far as we know, these were all associated with an extensive belt of bad weather (cold fronts and stationary fronts) which covered much of the country during that period, and the accidents involved ceilometers and solid structures alike. Accidents known to us occurred as far south as Macon, Georgia (David W. Johnston, letter: Nov. 1, 1954), as far north as New York City, where many migrants were killed at the Empire State Building (*New York Times,* Thursday, October 7, 1954, p. 1) and elsewhere, and as far west as Smoky Hill Air Force Base at Salina, Kansas (ceilometer, October 7, some birds received at the University of Kansas). Some of the above, and incidents from a number of other localities, were mentioned in varying detail in *Audubon Field Notes* (vol. 9, no. 1, pp. 6, 10, 15, 17, 18, 32, February, 1955). Still other accidents occurred at Columbia, Missouri (Richard P. Grossenheider, verbal communication), and Topeka, Kansas (present paper). Some probably have escaped our notice; summaries of some of these will probably appear in ornithological journals for some time to come. At Robins Air Force Base near Macon, Georgia, at least 50,000 birds were killed, of which about 2500, representing 54 species, were picked up (Johnston, *loc. cit.*).

ACCIDENTS AT TOPEKA, KANSAS.—At Topeka, Shawnee County, Kansas, all birds were killed by collision with the newly-erected (1954) television transmitting tower of station WIBW-TV. This tower is one mile west of the city.

The first casualties (see Table 1 for all others) were a Sora (*Porzana carolina*) and a Yellow-bellied Flycatcher (*Empidonax flaviventris*) found on September 7. The major accidents, however, occurred on the nights of September 24-25, September 30-October 1, October 5-6, and October 6-7. Totals of birds picked up (probably over 95 per cent of birds killed) are given in Table 1, in which each date given is that of the day after the kill, *i. e.*, the date on which the birds were collected.

All major kills occurred on cloudy and foggy nights associated with frontal weather. Throughout the period a few birds struck the tower even on fairly clear nights, and minor but appreciable "falls" occurred on the nights of October 4-5, 7-8, and 22-23. A few birds killed probably were overlooked for a time and found their way into later samples. This is especially probable in the case of some birds entered under date of October 23, as many of these were somewhat desiccated. Weights clearly altered by desiccation or mutilation were not recorded. Reports of these accidents have been published by Carson (1954 a, b, and c).

According to Carson (1954c:27), the majority of birds killed on nights of heavy flight fell "between three and four o'clock in the morning when skies were overcast and a cool front moved in from the north. Due to the cooperation of the watchmen it is thought that most of the birds that were killed were recovered. Of course some injured birds in hiding were not found and some were lost to predators."

DESCRIPTION OF WIBW-TV TOWER.—The tower is 950 feet tall and stands on a hill approximately 1000 feet above sea level· The fact that the tower is on a hill places the top of the tower at 1010 feet above the elevation of the average local terrain. The tower is triangular in cross-section, each face seven feet wide, and is constructed of six-inch steel L-beams with three-inch cross-members every seven feet and smaller diagonal cross-members. It has no taper and bears a transmitting antenna on the top. The tower is supported by 12 guy wires, 3 wires attaching at each of 4 levels. The cables extend south, WNW, and NNE from the tower and are 1½ inches in diameter. The tower is lighted by a series of red lights, some flashing and others steady. The transmitter was not in operation when the accidents took place.

WEATHER CONDITIONS.—All major kills at Topeka occurred when migrating birds encountered either a cold front or a stationary front lying over eastern Kansas. Typically, this frontal weather included rain, fog, and cloud ceilings down to as low as 800 to 1000 feet. Weather of this type presumably forces the migrating birds to fly below the cloud ceiling and thus brings them within the altitudinal range of the television towers.

Acknowledgments

We gratefully acknowledge our debt to the Topeka Audubon Society for making this study possible by carefully collecting birds killed at the television tower. L. B. Carson deserves special mention for his general supervision of the bird collecting by the members of the Topeka Audubon Society. Members of the Society and others who picked up birds under the television tower were: Mrs. Lloyd Biggs, Elaine Carson, L. B. Carson, Jesse A. Eddy, Elizabeth Fisher, Mrs. Walter Huxman, Florence McKinney, Mrs. Charles Martin, Mrs. Fred P. Martin, T. W. Nelson, Fred Prebble, Grace Prebble, Orville Rice, Mrs. G. Warren Scholl, E. W. Senne, and Beatrice Swenson

We received equally important assistance from students and staff of the University of Kansas in recording of data and preparation of specimens. The following helped in these ways: Rollin H. Baker, R. W. Dickerman, David L. Hardy, J. W. Hardy, Jane S. Mengel, Larry D. Mosby, Richard Van Gelder, South G. Van Hoose, and Glen E. Woolfenden. We are indebted to the Interlibrary Loan Service of the University of Kansas Library for help in securing certain reference works. Robert Sokal of the University of Kansas gave helpful advice concerning statistical procedures.

Notes on the Species Killed at Topeka

A list of numbers and kinds of birds killed is given in Table 1. Discussion of data afforded by certain species for which large samples were available will be found below. There are additionally certain data afforded by the sample and certain comments to be made on various species which can be handled most conveniently in an annotated list. In this list we have included all weight data (still scarce for many North American birds), comments on status in Kansas of various species, results of comparisons to determine subspecies, and miscellaneous observations. Weights of birds are given in grams and were taken on a triple-beam balance. Fat condition is given in the scale proposed by McCabe (1943: 556). Weight data from birds migrating at night should be especially useful because these migrants all have relatively empty crops and stomachs, thus reducing variability. Not all birds were suitable for weighing and measuring, for a variety of reasons. This accounts for discrepancies in totals between Table 1 and the annotated list.

All passerine species were aged by noting the degree of ossification of the skull. In no case, of the more than a thousand passerines aged by examination of the skull, did we find difficulty in determining whether an individual was a bird of the year or an adult. We found no specimens in which ossification of the skull was nearing completion. In the several species in our sample with distinctive first-winter plumages, we found complete agreement in age as shown by plumage and by condition of the skull. We think this is further proof, if such is needed, that this method of aging is thoroughly reliable in early autumn for the passerine species included in our sample and for others with similar breeding seasons.

TABLE 1.—BIRDS KILLED AT A TELEVISION TOWER AT TOPEKA, KANSAS, IN 1954

See annotated list for division into sex- and age-classes. Where discrepancies exist between totals given here and totals given in the annotated list, these result from the fact that some specimens could not be sexed and aged.

	Sept. 25	Oct. 1	Oct. 3	Oct. 4	Oct. 5	Oct. 6	Oct. 7	Oct. 8	Oct. 9	Oct. 10	Oct. 23	Totals
Pied-billed Grebe	...	1	...	...	...	1	...	...	1	...	...	3
Green Heron	...	...	...	...	...	1	...	...	...	...	...	1
Blue-winged Teal	...	1	...	...	...	1	6	...	...	...	...	8
Virginia Rail	...	3	...	...	...	1	...	...	...	...	...	4
Sora	1	6	...	...	...	1	1	1	...	...	...	10
American Coot	...	...	...	...	...	3	...	...	...	...	...	3
Mourning Dove	...	8	...	...	1	...	...	...	...	...	1	10
Yellow-billed Cuckoo	...	...	...	...	...	1	...	...	...	...	...	1
Black-billed Cuckoo	...	...	...	...	...	...	1	...	...	...	...	1
Yellow-shafted Flicker	3	...	...	...	...	...	...	...	...	...	...	3
Yellow-bellied Flycatcher	...	...	...	...	...	...	1	...	...	...	...	1
House Wren	2	3	...	...	...	1	2	1	...	1	...	10
Long-billed Marsh Wren	...	1	...	...	...	1	1	...	...	...	...	3
Short-billed Marsh Wren	1	2	...	...	...	...	1	...	...	...	...	4
Catbird	1	28	1	...	1	6	6	...	...	...	...	43
Brown Thrasher	...	1	...	...	...	1	...	1	...	...	...	3
Wood Thrush	...	3	...	...	...	...	...	...	...	...	...	3
Hermit Thrush	...	...	...	...	...	...	...	...	...	1	...	1
Olive-backed Thrush	...	14	...	1	...	...	1	...	...	...	...	16
Golden-crowned Kinglet	...	...	...	...	...	...	...	...	...	1	5	6
Ruby-crowned Kinglet	2	1	...	...	...	...	8	1	1	...	1	14
Yellow-throated Vireo	...	1	...	...	...	...	...	...	...	...	...	1
Blue-headed Vireo	1	19	...	1	2	5	8	3	1	...	...	40
Red-eyed Vireo	18	36	...	...	2	13	2	3	...	...	1	75
Philadelphia Vireo	3	9	...	...	...	...	...	...	...	...	...	12
Warbling Vireo	8	19	1	...	4	1	1	...	...	...	...	34
Black and White Warbler	1	1	...	...	...	3	...	...	...	...	...	5
Tennessee Warbler	...	1	...	...	1	2	1	...	...	...	...	5
Orange-crowned Warbler	7	14	...	...	1	4	19	5	1	1	...	52
Nashville Warbler	7	94	4	...	3	39	27	5	...	1	1	181
Parula Warbler	...	...	...	...	...	...	1	...	1	...	...	2
Yellow Warbler	3	3	...	...	...	1	1	...	...	...	...	8
Magnolia Warbler	...	1	...	...	...	2	...	...	...	...	...	3
Black-throated Blue Warbler	...	...	...	...	...	...	2	...	...	...	1	3
Myrtle Warbler	...	...	...	...	...	...	...	...	1	...	...	1
Black-throated Green Warbler	...	...	...	...	...	...	...	...	...	1	...	1
Chestnut-sided Warbler	...	1	...	...	...	...	...	...	1	...	...	2
Bay-breasted Warbler	1	...	...	...	...	2	...	...	...	...	...	3
Palm Warbler	3	...	...	...	...	...	...	...	...	...	1	4
Oven-bird	4	21	...	...	...	2	3	1	...	...	1	32
Northern Water-thrush	...	5	...	...	...	...	...	...	...	1	...	6
Mourning Warbler	15	64	...	...	2	11	2	1	...	...	...	95
Yellow-throat	10	115	2	...	4	25	18	1	1	...	...	176
Yellow-breasted Chat	...	1	...	...	...	...	...	...	...	...	...	1
Wilson Warbler	1	2	...	...	...	...	...	...	...	...	...	3
Canada Warbler	...	2	...	...	...	...	...	...	...	...	...	2
American Redstart	1	...	...	...	...	...	...	...	...	...	...	1
Bobolink	...	4	...	...	...	...	...	...	...	...	...	4
Rose-breasted Grosbeak	...	2	...	...	...	...	...	...	...	...	...	2
Indigo Bunting	...	1	...	...	2	3	1	...	...	...	...	7

Table 1.—*Concluded*

	Sept. 25	Oct. 1	Oct. 3	Oct. 4	Oct. 5	Oct. 6	Oct. 7	Oct. 8	Oct. 9	Oct. 10	Oct. 23	Totals
Dickcissel	...	31	...	...	1	3	1	...	...	...	...	36
Savannah Sparrow	1	6	...	1	...	1	5	1	...	...	1	16
Grasshopper Sparrow	...	7	...	...	2	3	3	1	1	...	1	18
Leconte Sparrow	...	...	...	...	...	...	...	...	...	...	3	3
Sharp-tailed Sparrow	...	...	...	...	...	1	1	...	...	1	...	3
Slate-colored Junco	...	...	...	...	...	...	...	...	...	...	1	1
Clay-colored Sparrow	...	11	1	...	...	2	...	1	...	...	...	15
Fox Sparrow	...	...	...	...	...	...	...	...	...	...	1	1
Lincoln Sparrow	...	41	7	...	...	5	22	3	1	...	3	82
Swamp Sparrow	...	1	...	...	...	...	1	2	...	...	...	4
Song Sparrow	...	...	...	...	...	...	...	...	...	...	2	2
Total—species	22	41	6	3	13	31	29	16	10	8	15	61
Total—individuals	94	585	16	3	26	146	147	31	10	8	24	1090

The annotated list may be consulted for further data in connection with the species listed in Table 1. As is indicated below, we regard the figures of this sample as unreliable to an unknown degree in comparing the relative abundance of one species with another. Accumulation of such data from various localities, however, should prove useful in another type of comparison. Samples of the same species killed in the same way at about the same time at different localities should be directly comparable. Eventually, this should provide us with a means of determining relative abundance of a species in different parts of its migratory route.

Approximately 200 of the most interesting specimens were preserved as study skins and are in the University of Kansas Museum of Natural History. An effort was made to preserve at least one of each species, and we fell only a few short of this goal. All of the forms rare in Kansas are represented by skins. We could see no reason to list the preserved specimens in detail here. Species of which no study skins were made, however, are so marked.

So far as we can tell, no truly western subspecies (from west of the Great Plains) occurred in the Topeka sample. Probably most or all of the birds came from areas more or less directly north of eastern Kansas.

In critical areas where different subspecies of the same species occur together in migration, data from samples of this kind should prove enlightening. In future analyses, conducted in such areas, it might be possible to preserve all specimens of some of the variable species, or at least to measure all individuals of species in which size is the most important variable character. Quantitative study could then be made of the different geographic variants occurring, their proportions in the migrant population determined, and their origins deduced. In studying populations of Painted Buntings (*Passerina ciris*) wintering in Mexico, Storer (1951) has provided an interesting demonstration of methods which can be applied to such samples.

A few bats killed at the tower provided a surprise. They will be discussed separately by Richard Van Gelder.

Podilymbus p. podiceps. Pied-billed Grebe.—Weights: male, 394.8 (all weights in grams); females, 332.5, 289.7; all fat.

Butorides v. virescens. Green Heron.—Weight: 1 (unsexed), 168.6.

Anas discors. Blue-winged Teal.—Weights: 4 males, mean 421.2 (391.3-458.1); 3 females, 367.7, 371.6, 393.2; all fat.

Rallus limicola. Virginia Rail.—Weights: 3 males, 73.7, 83.2, 90.5; 1 female, 67.3; moderately fat to fat.

Porzana carolina. Sora.—Weights: 4 males, mean 76.8 (68.7-89.9); 3 females, 62.6, 63.2, 63.5; moderately fat to very fat.

Fulica americana. American Coot.—Weights: 2 females, 385.3, 530.0, both fat. None preserved.

Zenaidura macroura marginella. Mourning Dove.—Weights: 2 adult males, 121.8, 140.2; 3 immature males, 113.1, 126.1, 130.0; 3 adult females, 122.5, 126.9, 136.0; 2 immature females, 129.4, 132.7; moderately fat to very fat. The presence of Mourning Doves in the sample is interesting as these birds are not generally regarded as night migrants. Conceivably the specimens were local birds going to roost. None preserved.

Colaptes auratus luteus. Yellow-shafted Flicker.—Weights: 2 males, 126.0, 139.4, little fat. Flickers have several times been recorded as night migrants.

Empidonax flaviventris. Yellow-bellied Flycatcher.—Weight: 1 immature male, 11.9, moderately fat. This is a rare species in Kansas, the present being the ninth preserved specimen for the State.

Troglodytes aëdon parkmanii. House Wren.—Weights: 4 adult males, mean 10.5 (9.8-10.9), 2 immature males, 9.0, 11.3; 1 adult female, 9.9, 1 immature female, 7.0; no fat (im. ♀) to fat.

Telmatodytes palustris dissaëptus. Long-billed Marsh Wren.—Weights: 1 adult male, 10.8; 1 adult female, 9.2; both moderately fat. The specimens are moderately bright and rufescent above, being typical of the populations of the central plains.

Cistothorus platensis stellaris. Short-billed Marsh Wren.—Weights: 1 immature male, 8.2; 1 adult female, 8.1; immature female, 8.2; all fat.

Dumetella carolinensis. Catbird.—Weights: 6 adult males, mean 37.5 (34.1-42.5), little fat to very fat; 14 immature males, mean 37.57 ± .94 (standard error), S. D. (standard deviation) 3.37, little fat to fat; 11 adult females, mean 39.09 ± .94, S. D. 2.97, little fat to fat; 12 immature females, mean 38.42 ± .83, S. D. 2.74, moderately fat to fat.

Toxostoma r. rufum. Brown Thrasher.—Weight: 1 immature male, 60.2, little fat.

Hylocichla mustelina. Wood Thrush.—Weights: 1 adult male, 54.2, moderately fat; 2 adult females, 44.6, 45.7, little fat and fat, respectively.

Hylocichla ustulata swainsonii. Olive-backed Thrush.—Weights: 6 immature males, mean 31.0 (28.1-33.2), little fat to fat; 6 adult females, mean 29.6 (27.1-35.0), moderately fat to fat; 3 immature females, 27.1, 33.8, 35.8, little fat to fat. The absence of adult males in our sample of 15 birds is noteworthy but inexplicable with our few data.

Regulus s. satrapa. Golden-crowned Kinglet.—Weights: 1 adult male, 6.7, moderately fat; 2 immature males, 6.5, 7.4, moderately fat and fat; 2 adult females, 7.3, 7.4, moderately fat and fat; 1 immature female, 7.2, moderately fat.

Regulus c. calendula. Ruby-crowned Kinglet.—Weights: 3 adult males, 6.2, 7.6, 8.2, little fat to fat; 1 immature male, 6.6, fat; 4 adult females, mean 6.1 (5.6-6.7), moderately fat to fat; 3 immature females, 5.8, 6.6, 7.0, moderately fat to fat.

Vireo flavifrons. Yellow-throated Vireo.—Weight: 1 immature male, 21.5, very fat.

Vireo s. solitarius. Blue-headed Vireo.—Weights: 9 adult males, mean 17.7 (16.6-19.5), little fat to very fat; 17 immature males, mean 17.53 ± .46, S. D. 1.83, no fat (13.8) to very fat (21.3); 7 adult females, mean 17.6 (15.0-21.6), moderately fat to very fat; 6 immature females, mean 17.0 (14.5-18.9), moderately fat to fat. Surprisingly numerous in the sample.

Vireo olivaceus. Red-eyed Vireo.—Weights: 1 adult male, 16.1, moderately fat; 38 immature males, mean 21.21 ± .43, S. D. 2.60, little fat (1 specimen) to excessively fat, mostly moderately fat or fat; 2 adult females, 18.1, 18.1, both fat; 23 immature females, mean 19.28 ± .46, S. D. 2.16, little (2 specimens) to very fat, mostly fat.

Wing length: 1 adult male, 79.1; 38 immature males, mean 78.05 ± .30, S. D. 1.80; 2 adult females, 76.3, 79.0; 23 immature females, mean 75.83 ± .42, S. D. 1.99.

As mentioned below, the presence of only 3 adults in the sample of 64 Red-eyed Vireos is highly significant and their occurrence only in the earlier samples is strong evidence of early migration by the adults.

Vireo philadelphicus. Philadelphia Vireo.—Weights: 2 adult males, 12.1, 15.9, moderately fat and very fat; 2 immature males, 11.1, 13.2, fat and very fat; 2 adult females, 13.1, 14.2, both fat; 5 immature females, mean 14.1 (12.0-15.2), moderately fat to very fat.

This species previously has been collected in Kansas only twice. Both records are from Doniphan County in September, 1922. Field observers occasionally record the Philadelphia Vireo in eastern Kansas. Long (1940:450) calls it a "very rare migrant in the extreme east." Our sample of 12 birds killed on two nights (and probably after the peak of migration of this species) leads us to think that this vireo is actually a regular, but overlooked, migrant in fair numbers.

Vireo g. gilvus. Warbling Vireo.—Weights: 12 adult males, mean 15.92 ± .43, S. D. 1.44, moderately fat to very fat; 8 immature males, mean 16.64 (14.2-17.8), fat to very fat; 5 adult females, mean 16.1 (13.7-18.0), fat to very fat; 5 immature females, mean 15.4 (14.1-17.8), little fat to fat.

Wing length: 12 adult males, mean 73.08 ± .49, S. D. 1.64; 8 immature males, mean 71.15 (69.9-72.8); 5 adult females, mean 70.0 (69.2-71.0); 5 immature females, mean 68.4 (67.7-70.3).

Tail length: 12 adult males, mean 53.33 ± .53, S. D. 1.77; 8 immature males, mean 50.03 (47.1-51.3); 4 adult females, mean 48.6 (47.7-49.8); 5 immature females, mean 49.2 (47.3-53.0).

There is no indication that western birds (*V. g. swainsonii*) make up any part of this sample.

The sample of 34 Warbling Vireos is too small to show the significance, if any, of the 2:1 ratio of males to females in the sample. Adequate samples of this species, taken at intervals, would add interesting information on time of migration of the four sex- and age-classes.

Mniotilta varia. Black and White Warbler.—Weights: 1 adult male, 12.5, fat; 2 adult females, 10.0, 10.0, little fat, fat.

Vermivora peregrina. Tennessee Warbler.—Weights: 1 adult male, 10.9, very fat; 1 immature male, 12.9, very fat; 2 adult females, 9.1, 12.5, moderately fat and very fat. The relative scarcity of Tennessee Warblers in the sample is surprising. They are common in the area in spring.

Vermivora c. celata. Orange-crowned Warbler.—Weights: 9 adult males, mean 8.8 (7.7-10.9), little fat to fat; 13 immature males, mean 8.92 ± .15, S. D. .53, little fat to fat; 5 adult females, mean 8.8 (8.3-10.3), little fat to moderately fat; 17 immature females, mean 9.13 ± .08, S. D. .72, little fat to fat. Of the 19 Orange-crowned Warblers killed on October 7, 11 had little fat, 6 were moderately fat, and only 2 were fat. No one-night sample of any other warbler killed at Topeka had less fat than this group of warblers. Furthermore, our sample (including 11 males) from October 7 (all sex- and age-classes) averaged 8.81 grams; the sample of 13 (including only 4 males) from October 1 averaged 9.1 grams. If one can assume, for any one species, that individuals undertake nocturnal migration only when they are physiologically ready, and this includes a certain amount of fat as a fuel source (Wolfson, 1954), then this further assumption seems justified: birds killed in migration with little fat must have flown longer or farther or both than birds killed with more fat. No further speculation on this point is permissible with our data, but the possibilities for study of future large kills, especially where actual time of death of the birds is known, are obvious.

Vermivora r. ruficapilla. Nashville Warbler.—More Nashville Warblers were picked up at Topeka than any other species and they are discussed in detail elsewhere in this report. The four sex- and age-classes can be identified with fair accuracy on plumage characteristics alone. Adult males have a large amount of reddish-brown in the crown, not completely veiled by the gray tips of the crown feathers. Immature males have a smaller but distinct crown patch, usually completely veiled. All males, compared with females, are grayer on the sides of the head, have a more nearly white eye-ring, and show clearer yellow on the throat. Adult females differ from immature females in that they more often have a trace of rufous in the crown and tend to be brighter below than the immatures. Of 177 specimens, 20 were very fat, 108 were fat, 46 were moderately fat, and 3 had little fat.

Parula americana. Parula Warbler.—Weight: 1 adult female, 7.9, fat.

Dendroica petechia aestiva. Yellow Warbler.—Weights: 1 immature male, 10.2, fat; 3 adult females, 8.8, 9.5, 10.1, moderately fat; 2 immature females, 9.0, 9.4, little fat and fat.

Dendroica magnolia. Magnolia Warbler.—Weights: 1 adult female, 9.0, moderately fat; 2 immature females, 7.9, 10.3, moderately fat and fat.

Dendroica c. caerulescens. Black-throated Blue Warbler.—Weights: 2 immature males, 13.8, 14.1, excessively fat; 1 immature female, 11.4, fat. This species is rare in Kansas. Although its breeding range is almost entirely east and north of Kansas, records in files at the Universtiy of Kansas show that more specimens have been taken in western than in eastern Kansas.

Dendroica c. coronata. Myrtle Warbler.—Weight: 1 immature female, 11.6, fat.

Dendroica pensylvanica. Chestnut-sided Warbler.—Weights: 2 immature females, 8.1, 10.0, little fat. Only one specimen from Kansas had been preserved previously although the species is a regular transient in small numbers throughout the state.

Dendroica castanea. Bay-breasted Warbler.—Weights: 1 adult male, 19.2, excessively fat; 1 adult female, 11.7, little fat; 1 immature female, 11.2, moderately fat. Only 5 specimens of this warbler have been taken previously in Kansas, 4 in spring (Ruth, 1952:18-19) and 1 in fall.

Dendroica p. palmarum. Palm Warbler.—Weights: 2 immature males, 9.9, 10.9, moderately fat; 2 unsexed immatures, 9.1, 9.4, moderately fat. This species has been taken in fall in Kansas only once before (KU 26353, taken by Wetmore, at Lawrence, on October 5, 1907), but probably occurs regularly in both spring and fall migration.

Seiurus a. aurocapillus. Oven-bird.—Weights: 2 adult males, 22.5, 23.8, fat and very fat; 14 immature males, mean 21.89 ± .66, S. D. 2.46, fat to very fat; 8 adult females, mean 21.4 (18.3-25.7), moderately fat to fat; 6 immature females, mean 18.2 (15.6-20.0), moderately fat to fat.

Seiurus noveboracensis notabilis. Northern Water-thrush.—Weights: 3 immature males, 18.1, 18.6, 22.2, moderately fat to fat; 1 immature female, 22.2, fat. Referring these birds to *notabilis* is a somewhat arbitrary procedure. They display some intermediacy of characters and probably stem from a population, intermediate between *notabilis* and *noveboracensis,* occupying much of central North America (cf. McCabe and Miller, 1933).

Oporornis philadelphia. Mourning Warbler.—Weight data presented elsewhere. The birds killed at Topeka provide the latest fall dates for this species in Kansas. Fifteen were killed on September 25, 64 on October 1, 2 on October 5, 11 on October 6, 2 on October 7, and 1 on October 8. We find no other records later than September 15. Of 93 specimens examined, 1 was excessively fat, 22 were very fat, 45 were fat, 21 were moderately fat, and 4 had little fat. The abundance of this secretive species in the sample was a great surprise. It had previously been considered a rather rare migrant in this area.

Geothlypis trichas occidentalis [>brachidactyla?]. Yellow-throat.—Weight data presented elsewhere. This species was second in numbers only to the Nashville Warbler in the total kill at Topeka. Of 167 birds examined, 29 were very fat, 114 were fat, 23 were moderately fat, and 1 had little fat.

The Yellow-throats are greatly in need of meaningful and comprehensive revision, which to date has been restricted to the western subspecies (Behle, 1950). Since the appearance of the 1931 A. O. U. Check-List a great deal of scattered taxonomic work on the species, as yet unsynthesized, has made the picture of its geographic variation a blurry one so far as the details are concerned. Made in the absence of adequate comparative material, the above identification is to be regarded as tentative. Also, it is, unfortunately, based only on those 6 of our 176 specimens preserved as skins. Five of these are adult males, the sixth being an immature female. Compared with a series of Kentucky specimens regarded as typical *brachidactyla,* these birds are paler and brighter above (tending toward gray-green rather than brownish olive), brighter and more extensively yellow below, with broader, more nearly white superciliary stripes above their black masks (in males). In size they are close to *occidentalis* (see Behle, 1950:202). Five males have an average wing-length of 56.6 mm. (53-59); one female measures 53. Six males from Kentucky: 55.1 (53-56); four females, 51.1 (48-56). Our birds may be assumed to have stemmed from a population to the north and west which, if not *occidentalis* (or *campicola* Behle and Aldrich, of which no comparative material is at hand), is intermediate between *brachidactyla* and more western birds. Judging from Behle's map (1950:fig. 32), these birds may have come from an area near the confluence of three subspecies (*campicola, occidentalis, brachidactyla*). Long (1940:452) reports three subspecies breeding in Kansas (*brachidactyla,* northeast; *occidentalis,* west; *trichas,* southeast). The occurrence in Kansas of *G. t. trichas* as currently understood is completely out of the question.

Icteria v. virens. Yellow-breasted Chat.—Weight: 1 unsexed immature, 29.7, moderately fat.

Wilsonia p. pusilla. Wilson Warbler.—Weights: 2 adult females, 7.5, 7.8, fat, moderately fat; 1 unsexed adult, 8.3, fat.

Wilsonia canadensis. Canada Warbler.—Weight: 1 immature female, 10.0, little fat. We know of only five other specimens from Kansas, although this warbler seems to be a regular migrant in small numbers in the state.

Setophaga r. ruticilla. American Redstart.—Weight: 1 immature female, 9.1, moderately fat.

Dolichonyx oryzivorus. Bobolink.—Weights: 2 adult females, 39.5, 42.9; 2 immature females, 38.8, 42.0; all excessively fat. Specimens of the Bobolink previously have been taken in fall in Kansas only on September 20 and 24, 1933, near Lawrence, by Long and Preble (Long, 1934).

Pheucticus ludovicianus. Rose-breasted Grosbeak.—Weights: 1 adult male, 50.4, fat; one immature male, 54.5, very fat.

Passerina cyanea. Indigo Bunting.—Weights: 1 adult male, 18.4, fat; 2 immature males, 17.2, 17.2, fat and very fat; 2 adult females, 14.3, 16.9, moderately fat and very fat; 1 immature female, 13.4, little fat. The sample was carefully checked for Lazuli Buntings (*Passerina amoena*); none was found.

Spiza americana. Dickcissel.—Weight data presented elsewhere in this paper. Dickcissels were picked up at the television tower on October 1 (31), 5 (1), 6 (3), and 7 (1). These birds, together with an adult female taken 3 miles east and 3 miles south of Lawrence, on October 11, 1953, by Tordoff, are the only specimens of this species taken as late as October in Kansas. The Dickcissel becomes inconspicuous in late summer and many observers here and elsewhere have thought the species disappeared much earlier than it really does (see Ganier, 1949). Of 34 specimens, 20 were very fat and 14 were fat.

Passerculus sandwichensis nevadensis. Savannah Sparrow.—Weights: 1

adult male, 19.4, fat; 2 immature males, 18.3, 19.0, moderately fat; 5 adult females, mean 17.2 (14.8-19.5), little fat to fat; 4 immature females, mean 18.0 (16.9-19.6), moderately fat to fat. Many of the Savannah Sparrows migrating through Kansas have in the past been referred to the subspecies *P. s. anthinus* (= *alaudinus* of the 1931 A. O. U. Check-List) by various workers (see Long, 1940:454). As Peters and Griscom (1938:464-5) have shown, true *anthinus*, breeding in the far northwest, ordinarily occurs in migration only in the western part of the country, the breeding Savannah Sparrows of a large part of the central continental region (east to southern Wisconsin) being *P. s. nevadensis* as now understood. Migrants of this pale, clay-colored subspecies should be abundant in Kansas, and all of the specimens in the present sample are referable to it.

Ammodramus savannarum perpallidus. Grasshopper Sparrow.—Weights: 3 adult males, 16.4, 17.6, 20.6, moderately fat, fat, fat; 5 immature males, mean 18.1 (16.0-20.2), little fat to fat; 5 adult females, mean 17.9 (16.8-18.9), moderately fat to very fat; 5 immature females, mean 18.1 (16.8-20.6), fat to very fat.

Passerherbulus caudacutus. Leconte Sparrow.—Weights: 1 immature male, 11.2, moderately fat; 1 immature female, 12.2, moderately fat.

Ammospiza caudacuta nelsoni. Sharp-tailed Sparrow.—Weights: 2 adult males, 15.2, 17.1, moderately fat and very fat; 1 adult female, 13.3, little fat. Five specimens of this species have been taken previously in Kansas, all in October in the eastern part of the state. Additionally, several observers have reported birds seen but not collected. The three birds from Topeka were picked up on October 6, 7, and 10 and are the only specimens taken since 1907. Possibly our specimens from Topeka struck the tower on the same night. Tordoff noticed, upon preparation, that the specimens from October 7 and 10 showed progressive drying of the extremities and spoilage as compared with the bird picked up on October 6.

Junco hyemalis cismontanus. Slate-colored Junco.—Weight: 1 immature female, 16.4, little fat. Juncos of hybrid type, whether *J. h. hyemalis* × *J. oreganus* subsp. or true *J. h. cismontanus*, are fairly common in eastern Kansas.

Spizella pallida. Clay-colored Sparrow.—Weights: 2 adult males, 11.6, 12.2, both fat; 1 immature male, 11.8, fat; 1 adult female, 12.5, fat; 7 immature females, mean 11.1 (9.7-12.5), little fat to fat.

Passerella iliaca iliaca. Fox Sparrow.—Weight: 1 adult female, 29.4, little fat. A trifle grayer above than any of several Kentucky specimens, this bird nevertheless seems well within the range of variation of *iliaca*.

Melospiza l. lincolnii. Lincoln Sparrow.—Weights and measurements are discussed elsewhere. Of 81 specimens, 15 were very fat, 47 were fat, 12 were moderately fat, and 7 had little fat. Interestingly, there is no evidence that the large southern montane subspecies (*M. l. alticola*) has contributed to the present sample. No bimodality is evident in the curve of wing-length in our birds, the largest of which barely approach the small extreme recorded for *alticola* by Miller and McCabe (1935:156).

Melospiza georgiana ericrypta. Swamp Sparrow.—Weights: 3 immature females, 14.3, little fat, 16.7, 17.0, moderately fat. Swamp Sparrows examined were all more or less brightly colored and seem to belong to this northern subspecies.

Melospiza melodia juddi. Song Sparrow.—Weights: 1 adult female, 19.4, little fat; 1 unsexed immature, 16.0, little fat. A large proportion of the migrant and wintering Song Sparrows in eastern Kansas probably originate from the range of this subspecies in the northern plains. *Melospiza melodia euphonia.*—One immature female (not weighed) was picked up below the tower on October 27, 1954, and thus does not appear in Table 1. The specimen proved typical of this generally more eastern subspecies upon comparison with a large series from Kentucky. For what it may be worth we refer the single specimen to this subspecies. Long (1940:456) reported two eastern subspecies from Kansas (*"beata," melodia*). All Kansas specimens genuinely of eastern origin probably originate from the range of *euphonia,* as now understood.

Randomness of the Sample

The reliability of certain of the conclusions which might be drawn from data of the kind presented herein depends largely on the randomness of the sample. To what degree does this sample provide a true cross-section of the nocturnal migrants present over the area on a given night or succession of nights? As far as the relative abundance of species in the sample is concerned, there is little doubt that it is not at all random. The absence of such species as the Gray-cheeked Thrush (*Hylocichla minima*), among the passerines, and many of the shorebirds known to be migrating through the area at the time is evidence for this statement. Quite possibly many seminocturnal species did not strike the tower at all for the simple reason that they could see it, and certain large-eyed diurnal species (such as thrushes and shorebirds) may avoid collision to some extent, thus not appearing in the sample in proportion to their actual numbers. Finally, some or all of the species concerned probably migrate partly by day. The sample may to some degree reflect the true relative abundance of closely related species. For example, there is little doubt that, as shown by the sample, Nashville Warblers are more numerous locally at this season than Tennessee Warblers, a fact that can readily be corroborated by ordinary field observation. Also, the sample is useful in suggesting the actual abundance of species which are furtive and/or difficult to identify under normal field conditions, for example, the Mourning Warbler and Philadelphia Vireo. It is obvious that the sample should reflect the true relative abundance at one place and time of any two species with equal tendency to migrate by night and equal tendency to strike the tower. Since the facts in regard to both tendencies are at present unknown for most species, we think that interspecific comparisons should be avoided or approached with extreme caution.

In respect to the relative abundance of the various sex- and age-classes within a given species, the sample is, we think, as close to random as is possible to obtain. Certainly it is greatly superior to samples obtained by field collecting, where possible differences in habits, wariness, and experience of the birds, and subconscious (if not conscious) selection by collectors can all bias the results. Dwight (1900:128-9) believed that the greater wariness of adult birds was almost entirely responsible for the seemingly disproportionate number of immatures in autumn and gave some observational evidence in favor of his views. The large percentage of adults in some of the samples here treated tends to reinforce Dwight's position. To a somewhat lesser extent, this advantage in randomness of accidental kills over routine collecting may be supposed to apply also in demonstrating the composition by subspecies of a single migrant species.

So far as particulars already mentioned are concerned, the present sample or other samples of tower-killed birds would seem to be in no way superior (that is, more nearly random) to samples obtained in connection with lighthouses and other lighted objects, and ceilometers. In one important respect, however, it is probably somewhat superior to these as the dimly red-lighted structure has not been shown to have any important collecting or attracting influence. Thus, in computations intended to estimate the over-all abundance of migrants, the sample should be more reliable than samples involving bright light with its possible attracting effect.

Number of Migrants

If it can be assumed that nocturnally migrating birds are approximately uniformly spaced across the sky and that the red lights did not attract birds which would otherwise have missed the tower, it is possible to compute the volume of migration from the sample killed. In regard to the first assumption, both Stone (1906:250-251) and Lowery (1951:409-413) have presented evidence of fairly uniform distribution of nocturnal migrants. We have no information on the second assumption beyond the facts that birds do not strike the high towers on clear nights or lower towers even on stormy nights.

On nights when large numbers of birds struck the 950 foot Topeka tower, only a few struck a 500 foot radio tower, also lighted with red lights, at Lawrence, 24 miles east, under similar weather conditions. Most of the birds found at Topeka were fairly close to the base of the tower, indicating that they struck the tower itself or that they were flying high enough to strike guy wires only fairly close to the tower. The scarcity of birds under the guy wires some distance from the tower at Topeka and at the radio tower at Lawrence causes us to think that most of the birds were flying more than 450 feet above the ground. On this basis, we have computed numbers of migrants passing through a plane one mile long and 500 feet high (2,640,000 square feet), intersecting the assumed path of migration at right angles. Vertically, the theoretical plane begins at 450 feet above ground and has its top edge at 950 feet. The solid (discounting spaces between girders, *etc.*) cross-sectional area of the tower intersecting this plane was computed by actual measurement to be 1685 square feet. On the night of September 30-October 1, 585 birds were killed. By computation ($585/1685 = X/2{,}640{,}000$), approximately 916,000 birds passed through the mile-long plane that night. On each of the nights of October 5-6 and October 6-7, approximately 230,000 birds passed through this plane. By comparison, Lowery (1951:436) recorded maximum station densities in one night in spring of 63,600 birds at Tampico, Mexico, and 51,600 at Lawrence, Kansas, as determined by moon-watching. Lowery's figures refer to numbers of birds crossing any part of a circle one mile in diameter and are roughly comparable to ours if, as we think, most of the birds at Topeka were flying at altitudes between 450 and 950 feet above the ground.

It must be realized that these figures are only approximations. One variable ignored is the frontal extent (or area, viewed from the front, subject to damage by striking an obstruction) of the birds themselves. Since practically all birds killed showed head or trunk injuries, rather than a high proportion with only broken wings, we chose to disregard frontal extent of the birds in our calculations. If our figures are inaccurate by as much as 50 per cent in either direction, which seems unlikely to us, they still give some idea of the tremendous volume of nocturnal migration under some conditions.

It may be more meaningful to compute numbers of migrants by species. This can be done readily by making appropriate substitutions from Table 1 in the equation given above. For example, on the night of September 30-October 1, approximately 147,000 Nashville Warblers passed through the mile-long plane and on the same night, 100,000 Mourning Warblers and 14,000 Philadelphia Vireos. Neither of the last two species would be judged to be abundant migrants in autumn in eastern Kansas by ordinary field observations; the television tower sample, however, indicates that these as well as other species must often be overlooked when they do stop in Kansas.

Differential Migration of Sex- and Age-classes

HISTORY OF THE SUBJECT.—For a long time it has been known in a general way that old and young birds and males and females of some species do not always migrate at the same times, by the same routes, or even to the same places. This is a subject about which much has been written. Reading the summaries of some general texts, it is easy to acquire the impression that the facts of the matter are well known. On the contrary, they are poorly known and much remains to be learned before differential migration is understood. This can best be indicated by a brief survey of the literature.

The importance of the subject was emphasized by Meinertzhagen (1930:52) in one of the later reviews of differential migration: "The main problem concerns the Cause of Migration, the Stimulus which compels Migration and the Origin of the Migratory Habit. . . . There is, however, a minor problem which affords valuable evidence in helping us to solve the major problem, bearing very directly on it, namely, the order of sex and age on migration."

The mystery of how birds, especially the young, find their way in migration has fascinated students since the earliest times. The quite natural though purely anthropomorphic conclusion of early scholars was that the old birds led the young on migration. This attractive idea persisted long after ornithology began to grow into a science. The classic theory was restated by Palmén (1876:267), in one of the first thorough reviews of the subject of migration, as follows: "Directe Beobachtungen in der Natur ergeben, dass die Schaaren von ziehenden Vögeln allgemein ältere und stärkere Individuen als Anführer des Zuges haben." Variously modified, this view continued to crop up for some time and still found support in the 1890's (see Dixon, 1892:69). Gätke (1895:101) correctly questioned the credibility of Palmén's "direct observations."

With the gradual abandonment of the unsupportable classic theory, diametrically opposed views were adopted by workers on opposite sides of the Atlantic. The American stand was ably expressed by Brewster (1886), who went to great pains to state his case and give evidence, and who was later supported by Allen (1896:144-147; 1909:17). The Americans held that adult birds nearly always preceded the young in migration, and this was based on much evidence, whether or not correctly interpreted. Dwight

(1900:127) also gave evidence in favor of this theory. Equally definite, if, as has later been shown, somewhat vaguely documented, was the famous work of Gätke (1895: see pp. 100-113), who after many years' observation of migrant birds in Heligoland concluded the exact opposite, that young in general precede adults (see critiques of Allen, 1896:144-147; Wiegold, 1926:5). Gätke's dissenting opinion was for a time supported enthusiastically by British workers (Gurney, 1923:579-580).

As so often happens, neither extreme has withstood the test of time, and more recent summaries (Meinertzhagen, 1930:55-56; Thomson, 1926, 1936:488-489; Wiegold, 1926) have tended to compromise. Many exceptions to Gätke's extreme conclusion have been detected. Exceptions to the Brewster-Allen stand have also been discovered, although work along these lines on the American side has lagged somewhat. Rowan (1926) has given further evidence on the migration of certain shorebirds, and some evidence has accrued in relation to particular species and groups as a result of life-history and banding studies (see Pitelka, 1946). Authors of major works on migration, however, have either been preoccupied with other phases of migration or avoided the issue. In an able study (one of several on related subjects) of the composition by sex and age of migrant populations in north Germany, Drost (1935: 177) did not go into the question of order on migration.

One is left with the impression that the whole subject is still unsettled. While earlier workers sought to reduce the entire matter to law, the latest disclaim the possibility of generalization. After summarizing Brewster's and Gätke's opinions, Thomson (1926:79) wrote: "It would seem, in any event, that no general rule can be laid down." Meinertzhagen's summation (1930:56-57) still represents fairly well the status of our knowledge: "Order of sex and age on autumn passage is very difficult to arrive at, as evidence is conflicting. But, on the whole, it seems that birds flock together, old and young, preparatory to moving south, and do in many cases initiate migration in company. . . . But once movement is initiated, among birds which do not habitually fraternise in flocks, adults, and especially males, will naturally outstrip the less virile females and still less virile offspring. . . . The consequence is that any observer at an intermediate station such as Heligoland is, in noting birds of the year as first arrivals, has not had an opportunity of noting the flocks of adults which have passed without alighting. On the other hand, there is very definite evidence to show that among certain species, adults follow their offspring on migration. The reason for different behaviour among different types of birds remains obscure." We regard much of this as still theory.

It would be difficult to imagine a better way of resolving the problems and uncertainties just reviewed than by the detailed analy-

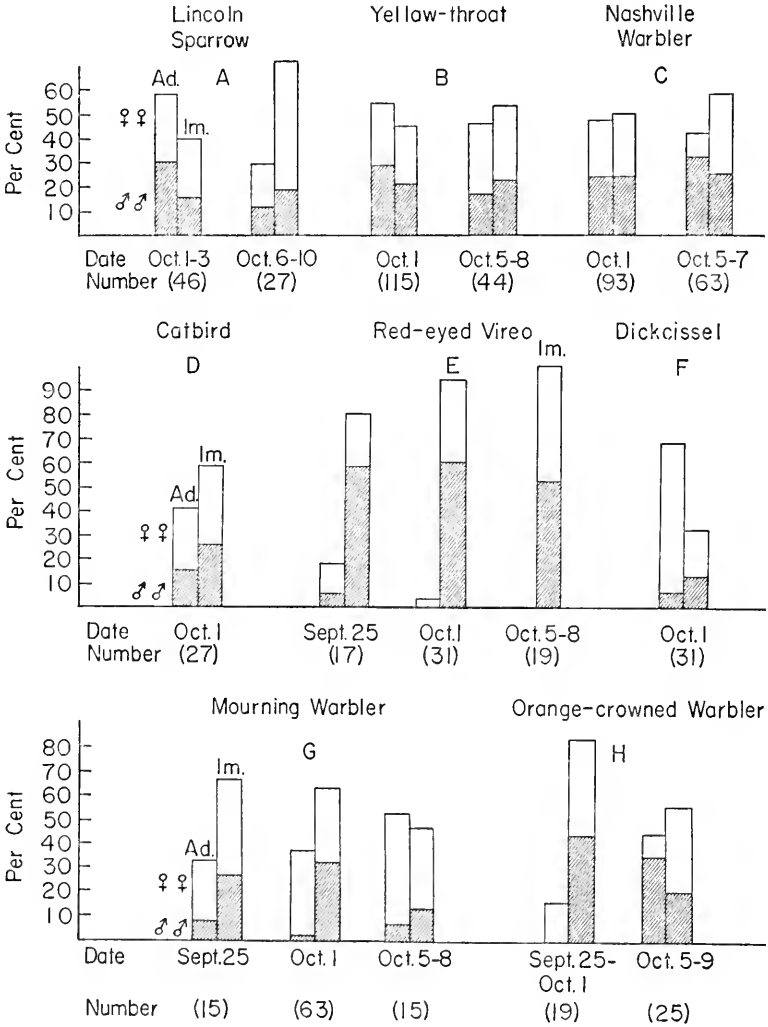


FIG. 1. Composition by age and sex as found in one or more series of each of eight species of birds included in the Topeka sample. Each separate series is represented by a single histogram, the histograms for a species being grouped with the earliest series on the left. Each histogram expresses the numbers of adults (left-hand column) and immatures (right-hand column) in terms of percentage of the whole series. Thus the two bars of each couplet add up to 100 per cent. The hatched portion of each bar represents males, the clear portion females.

sis of large samples of migratory birds killed at random at various points and times. An analysis of the sample of birds accidentally killed at Topeka is presented here as an initial step in this direction. Although the conclusions based on this sample are tentative and may in time be altered, the data themselves are definite. If this general type of analysis is repeated again and again—applied to samples taken on many dates and in many localities—a mass of hitherto unparalleled evidence for the study of migration will emerge.

Differential Migration of Sex- and Age-classes as shown by the Topeka Sample.—Smaller samples have not been treated. Species affording samples seemingly large enough to justify at least preliminary analysis were: Catbird, Red-eyed Vireo, Mourning Warbler, Dickcissel, Nashville Warbler, Orange-crowned Warbler, Yellow-throat, and Lincoln Sparrow (Fig. 1). For all of these except the Catbird and Dickcissel, at least two samples from a week or more apart were available for comparison in an effort to detect trends in migration. Fig. 1 shows the actual ratios of sex- and age-classes observed in samples of the species listed above. Each of the last four species provided two separate samples, of sufficient size to warrant an attempt at measuring the statistical significance of the observed changes in adult-immature ratios (Table 2).

Table 2.—Statistics of the Ratios of Adults to Immatures in Four Species

Species	Dates of samples	Total number	Number and percentage of adults[1]	Difference (in %)[2]	P[3]
Nashville Warbler	Oct. 1 (93) Oct. 5–7 (63)	156	45 (.484) 26 (.413)	.071	.36
Orange-crowned Warbler	Sept. 25–Oct. 1 (19) Oct. 5–9 (25)	44	3 (.158) 11 (.440)	.282	.05
Yellow-throat	Oct. 1 (115) Oct. 5–8 (44)	159	62 (.540) 20 (.455)	.085	.34
Lincoln Sparrow	Oct. 1–3 (44) Oct. 6–10 (27)	71	27 (.614) 8 (.296)	.318	.01

[1] Percentage of immatures equals 1.000 minus percentage of adults.

[2] Standard error of the difference between ratios was computed by the formula $\sigma_e = \sqrt{P_e Q_e \left(\frac{1}{N_1} + \frac{1}{N_2}\right)}$, where P_e equals percentage of adults and Q_e equals percentage of immatures in the entire sample.

[3] Probability of error; *i. e.*, a P of .01 means there is one chance in 100 that the difference observed does not represent an actual difference in nature.

Upon the application of statistical methods it soon became evident that, unless changes in ratio between two samples are marked, large samples would be required in order to reach conclusions of high statistical significance in a single study of the present type. In this case (see Table 2), the Lincoln Sparrow and Orange-crowned Warbler, though represented by only moderate-sized series, show marked changes in age composition over the period studied, and the statistical treatment indicates a high degree of probability that these changes are real. Assurance that the lesser changes observed in the Nashville Warbler and Yellow-throat are real, on the other hand, is much less, even though the samples are larger. Few if any of the samples here discussed are as large as might be desired. Therefore, conclusions based upon them (see below) are to be regarded as tentative. Many other, future, samples will perhaps also be insufficient in size in themselves. There are, however, statistical advantages to repetition which will serve to make the repeated analysis even of small samples significant and valuable.

Certain of the samples not treated statistically show ratios that can be seen by inspection to be probably significant. For example the almost complete absence of adults from the three samples of Red-eyed Vireos (Fig. 1E) cannot be disregarded in view of the size of the whole sample of the species. The same applies to the high percentage of adult females and the near absence of adult males in the sample of the Dickcissel (Fig. 1F). The continuity in direction of changes observed in the three samples of the Mourning Warbler (Fig. 1G) and Red-eyed Vireo is likewise probably significant, even though some of the samples compared are small. It seems to us that the application of statistical methods to these species should await the accumulation of more material. For anyone desiring to treat them statistically now, the data are inherent in this paper.

We have not computed the standard errors of the ratios of sexes within age groups (except experimentally in a few cases). This can easily be done, however, and the significance of a given ratio determined, on the assumption (perhaps sometimes dubiously justifiable) that the sex-ratio in the species concerned is one:one. Obviously there is no point in computation of the standard errors of adult-immature ratios in single samples (such as that of the Dickcissel) until the actual ratio prevailing in the species in nature at the season in question is known for comparison with the observed ratio. Our formal statistical treatment, therefore, has been limited to an examination of the significance of the *changes* between adult-immature ratios in samples of the same species taken a number of days apart.

The samples suggest several patterns of differential migration of sex- and age-classes. Indeed, the important consideration brought out—in our opinion not hitherto sufficiently emphasized in literature—seems to be that in generalizing about adults and immatures, one must be careful to take sexes into account, and conversely, in generalizing about males and females, one must consider also age. In other words, there are really four classes to be considered. This poses additional problems in analysis and introduces the need for still larger samples in order to reach significant conclusions. To illustrate: an adult-immature ratio of 40:20 ($N = 60$) may be satisfactorily significant, while within the 40 adults a ratio of 25 males:15 females may not be. Were the original sample 80:40 ($N = 120$) with male adults 50 and female adults 30, it is obvious that the significance of the latter ratio would be greater. The same applies in reverse if the greater emphasis is placed on sex and the lesser on age. Because of the moderate size of the samples this problem has been felt in the present study in respect to sex ratios within age groups, many of which must at present be regarded as of tentative significance.

In short, what the earlier ornithologists regarded as a simple problem is in reality a complex one. There are only two patterns in what may be called the Brewster-Gätke argument: adults first or immatures first (with of course the further possibility of both at the same time). Both patterns occur, as is now known, at least to some extent. But actual patterns, as suggested by our samples, are more complex when all classes are considered. It will readily be seen that, if adult males, immature males, adult females, and immature females be regarded as units, each with certain migratory characteristics, the combinations of these units in various orders of migratory precedence are potentially numerous. In fact, of course, they do not behave strictly as units (or perhaps very rarely so), but our data strongly indicate that the tendency exists in many cases. This may be stated another way. The present samples may be reduced to two basic patterns, fitting the classic early American (adults first) and early European (immatures first) theories. But, either such simple arrangement is compounded in some, perhaps in truth in all, instances by differential migration of the sexes *within* each age class. This proposition can also be stated backwards:

the samples show differential times of migration of the sexes, compounded by differential times of migration of the age groups within each sex. The order in which these matters are approached depends on what one is trying to find out. Influenced by the literature, in which most emphasis has been placed on age, we have approached the problem from that standpoint. The data and figures here given, however, can be juggled if one wishes to place first emphasis on the order of sexes in migration.

Bearing in mind what has just been said, particularly in respect to sizes of samples necessary for significance, let us consider the patterns of migration suggested by the Topeka sample. These are as follows:

(1) *An early migration largely composed of adults, giving way later on to a preponderance of immatures.* Regardless of variations among them, samples showing this basic pattern are in line with the opinions of Brewster (1886) and his followers. This pattern is here shown by the Lincoln Sparrow, Yellow-throat, Nashville Warbler, Catbird (one sample only), and Red-eyed Vireo (Fig. 1, A, B, C, D, E). The evidence of these and all other samples would admittedly be more conclusive if the samples were further apart in time or, better still, were there more of them. There is evidence that differences in migration of the sexes, within age classes, influence this pattern, sharply in some instances. In the later samples of Lincoln Sparrow, Yellow-throat, and Red-eyed Vireo (Fig. 1, A, B, E) there are relatively fewer males, both adult and immature, than in the earlier samples and this may be true also of the Catbird, judging from the single sample. The Red-eyed Vireo (Fig. 1, E) is characterized by small number, or absence of, males in each sample but the samples are not significantly different, and can be regarded as one. Although the samples of the Dickcissel and Mourning Warbler (Fig. 1, F, G) show a somewhat different overall pattern and are discussed further on, they also contain few adult males. Since these samples are from a period that is near the end of the migration of Red-eyed Vireos, Mourning Warblers, and Dickcissels, it may be assumed tentatively that the adult males have already migrated. Meinertzhagen (1930:56) postulated that in many species there is an earlier or more rapid migration of adults, particularly males, and the data for the above species in our sample tend to support his assumption. But our data suggest in addition that in some species *immature males* migrate earlier, or more rapidly, than do *immature females*, just as adult males precede adult

.females in some instances. Within this general pattern (adults first) another variation is shown by the Nashville Warbler (Fig. 1, C) in which the later sample of adults is heavily weighted towards males, even though an increasing over-all proportion of immatures is evidenced. In this case, and contrary to Meinertzhagen's suggestion, it would seem that adult females have preceded or outstripped adult males in migration.

(2) *An early preponderance of immatures, followed by a preponderance of adults.* The several species of birds at Topeka that display this pattern conform with the conclusions of Gätke and other early Old World ornithologists that in most species immatures precede adults in migration. In the present sample two variations of this pattern occur.

(a) In the Dickcissel (Fig. 1, F) and the Mourning Warbler (Fig. 1, G), immatures decrease more markedly than adults (visible in samples of Mourning Warbler; inferred in Dickcissel), leaving the adults in the majority in the closing phase of migration. The distinctive and interesting feature in each of these two species is the ascendancy in numbers of adults *despite* the almost complete disappearance of adult males. The relative increase of adults is here caused by a retarded migration of adult females, which linger conspicuously behind all other classes. Something of this nature was suggested, in theory, by Dixon (1892:70) who thought that adult females are delayed by "maternal duties." It was hinted at also by Dwight (1900:127) who thought that in some species females molted later than males as a result of prolongation of parental responsibilities. As mentioned already, there is need for caution in interpreting the present samples because the Dickcissel is represented only by one sample and two of the three samples of Mourning Warblers are small. In the case of the Mourning Warbler, the samples may be regarded as one, nearly lacking in adult males. The progressive increase of adult females, however, may be significant; at least there are enough of these to make division of the birds into three samples enlightening. There is, of course, some chance that the majority of adult males have not yet migrated, or are migrating by a different route. This seems unlikely in both cases. October 1 is late in the migration of the Dickcissel and it seems that large-scale migration would not occur much later, and in the case of the Mourning Warbler adult males are rare in all three samples, extending over a considerable period and reaching late into the probable migration period of the species. It is interesting to conjecture just when and where adult male Mourning Warblers do migrate in autumn. Brewster (1886:16) wrote: "This species arrives at Cambridge [Massachusetts] about September 12, and during the remainder of the month is . . . abundant . . . . The adults, however, are so very uncommon that I have never known them [to] represent more than five per cent of the total number of individuals. They do not seem to be more numerous in the earlier flights than towards the close of the month, and I am very sure that they cannot be found in this locality before the young begin to appear." While the present samples show an abundance of adult *females* of this species (could Brewster have failed to recognize these as adults?) the whereabouts of the adult males remains a mystery.

(b) Another variation is displayed by the Orange-crowned Warbler (Fig. 1, H). Here also there is an increase of adults towards the end of migration, but this increase is marked by a growing percentage not of females but of males. Locally this species is a late migrant compared with most others of the Parulidae. Thus the first sample, composed of birds taken September 25-October 1, may be regarded as fairly early in the fall migration. Immature birds compose 84.2 per cent of this sample, there being no adult males at all. By October 5-9 the picture has changed markedly, the sample being composed of 44 per cent adults (82 per cent of which, in turn, are males) and 56 per cent immatures. In view of this trend one can not help suspecting that a still later sample would show a majority of adults, perhaps nearly all males. This of course does not necessarily follow; the migration of immatures could simply be more protracted, and could have commenced earlier, than that of adults.

Little imagination is required to see how enlightening it might be could we analyze thoroughly the patterns of all migrating species. When the detailed facts are available, it seems likely that general trends will emerge which may be of great significance to the study of migration in general. A final point which must eventually be clarified is determination of the extent of variability in the pattern of each species from year to year and locality to locality.

Once patterns of precedence in migration of different classes are established, search into the life-histories of the species concerned may help to explain the peculiarities discovered. In the present case, for instance, we find a possible clue to the reason for the high proportion of adult females of the Dickcissel late in migration, as shown by our sample. Gross (1921:14-15) presented evidence that adult female Dickcissels molt considerably later than their mates, and we have independent evidence that individuals of this species are at times almost flightless when molting the remiges!

Molt in Relation to Migration

GENERAL COMMENT.—The exact relationship between molt and migration seems not to have been definitely established. The subject has received cursory attention in the literature and conflicting opinions have been expressed. Dwight (1900:126-128) believed that molt is completed or nearly completed before migration in nearly all passerine species that occur in New York save for certain swallows and flycatchers. Molt has since been found to precede migration of at least one of the flycatchers (*Empidonax virescens*) considered by Dwight to be an exception to this rule (Mengel, 1952). In Great Britain the subject of molt in migration was considered in some detail by Rintoul and Baxter (1914) and Ticehurst (1916), who arrived at conclusions similar to Dwight's. These workers also found certain swallows to be exceptions to the rule.

The above authors and others have shown that, at least among passerines, some body molt is frequently found in migrating individuals but that molt of tail feathers is much less often found and molt of remiges almost nonexistent. Baxter and Rintoul noted only four cases of molting wing feathers among hundreds of migrants. Among the diverse non-passerine orders the picture seems to be more complicated, as might be expected. We do not, however, comprehend the reasoning which led Meinertzhagen (1930:56) to summarize: ". . . on the whole it can be said that though birds seldom migrate when flight feathers are in quill, moult in general does not influence migration." This seems to us an obvious *non sequitur.* Meinertzhagen (*loc. cit.*) went on to say: "Males and females of one species are believed to moult simultaneously [see, however, Dwight, 1900:127], and there is no doubt that in some cases the two sexes migrate at slightly different times, and occasionally prefer different winter quarters. Birds of the year never moult their quills previous to their first autumn migration [Consultation of Dwight, 1900, who gives many examples of this, would have spared Meinertzhagen this error.], and yet they frequently follow adults on passage and sometimes precede them. There are no grounds for believing that adults have moulted their quills before birds of the year are prepared to migrate [but there are, in many cases; *cf.* Dwight, 1900:127], in the case where adults precede the latter. Neither is there any evidence to show that adults have not moulted their quills till after their offspring are ready for passage, in the case where they follow their offspring. It does not, therefore, appear that moult is an important factor."

Comments interpolated above show our feeling that this summary is inadequate and misleading. To us it seems that the extreme rarity in migration of birds with remiges in molt is strong evidence that molt *does* influence at least the time of migration. It is immaterial whether this molt occurs before or after migration, although in the majority of cases it seems to take place before. Much more needs to be known of the migration pattern and molt of each species before generalizations can safely be made.

Analysis of samples of migrants can show only the presence and nature or the absence of molt in birds actually migrating. In the present instance shortage of time and manpower for preserving some and processing all of the sample resulted in incomplete data being kept on molt. We include this section to emphasize uncertainties still prevalent and to stimulate further work.

MOLT IN THE TOPEKA SAMPLE.—Our limited findings coincide with those of Rintoul and Baxter (1914). Body molt was noted in a number of individuals and species. When present, this molt almost invariably was in its final stages. One immature male Rose-breasted Grosbeak (October 1) was in heavy body molt. It is perhaps worthy of mention here that this grosbeak evidently migrates at times in extensive molt. An adult male (RMM 1102) taken by Mengel near Henderson, Kentucky, on September 9, 1949, was molting plumage of body, wings, and tail, no feather of the last being longer than one half inch. This remarkable specimen had only five primaries on one side and four on the other fully functional. The outermost on the left and two outermost on the right were from the previous plumage, not yet dropped; the three innermost of each wing were new and full-length.

In the present sample molt of remiges was noted in one specimen, an adult female Indigo Bunting (October 1) with outer primaries sheathed and with molt in progress in the body plumage. The one (immature) Yellow-breasted Chat in the sample (October 1) had all of its tail feathers nearly full-length but in quill, possibly as a result of accident, and two feathers were being replaced also in the tail of an immature Clay-colored Sparrow (October 6), which was also in body molt and had some juvenal feathers on the belly and flanks.

Body molt near completion was further noted as follows: immature male Yellow-throated Vireo (October 1), adult male Blue-headed Vireo (October 1), immature female Leconte Sparrow (October 23), several Lincoln Sparrows (various dates).

Size Differences according to Sex and Age

LINEAR MEASUREMENTS.—Taxonomists long have recognized in many species that males differ in size from females. Less attention, until recently, has been paid to the relative sizes of adult and immature birds. Many taxonomists, however, seem to have had an uneasy suspicion that immature birds are "untrustworthy" in comparison with adults, and immatures have often been excluded from samples when recognizable. Since, however, there are still relatively few reliably aged specimens in collections, for the most part only those immature birds immediately recognizable as such by obvious plumage differences (which are often present only in juvenal plumage) have been excluded from series. The majority of birds in first winter plumage so closely resemble adults that the two ages have been included in series for measurement. In most passerines these younger birds still bear the juvenal feathers in wing and tail and are, in size of these important parts, quite as "untrustworthy" as birds still in juvenal body plumage. Even if a complete postjuvenal molt occurs we still should not assume that first winter feathers are as long as adult winter feathers without first determining that this is so. Although aware of this problem, systematists until recently seemingly have been more or less content to disregard it, or forced to do so for practical reasons. Miller (1941:179) had little choice but to hope that size differences between adult and immature juncos were unimportant. Behle (1942: 217) wrote of Horned Larks, *Eremophila alpestris:* ". . . the plumages of first-year birds and adults seem indistinguishable, though I have never quite satisfied myself that there are no differences in lengths of rectrices and remiges." He added, with logic confusing to us: "Since it is a difficult problem to determine the ages of horned larks that have passed the postjuvenal molt, this similarity of plumages is fortunate for the systematist."

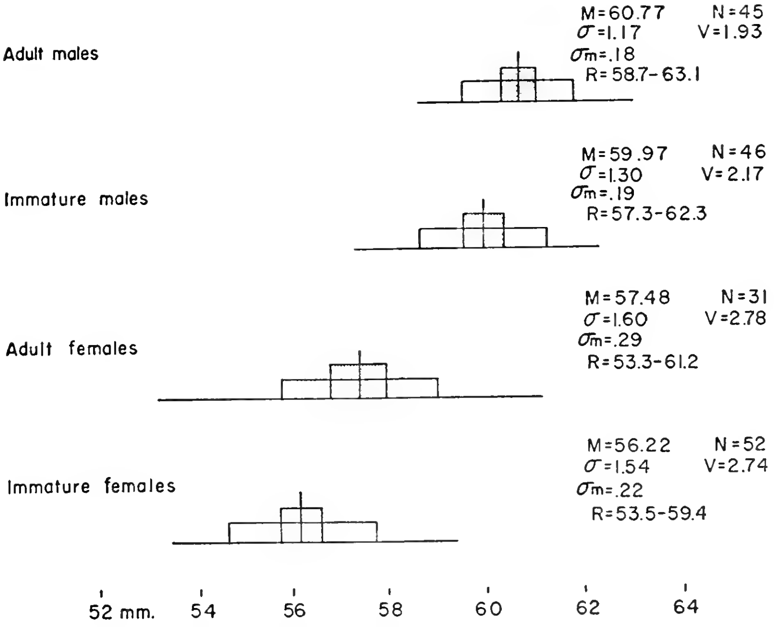
In recent years, some workers have analyzed size differences between adults and immatures. Sibley (1950:115) showed that adult Red-eyed Towhees (*Pipilo erythrophthalmus*) had notably longer wings and tails than immatures, and the same was demonstrated in Red Crossbills (*Loxia curvirostra*) by Tordoff (1952). In work with jays (*Aphelocoma*), Pitelka (1951:199) found that: ". . .

in comparisons of dimensions of sex and age groups within a given sample, although magnitude of difference varies from one character to another, most of the averages are successively smaller for first-year males and adult and first-year females." He listed exceptions and concluded: "Segregation [of sex and age classes] has proved to be of extreme significance in an interpretation of individual and geographic variation."

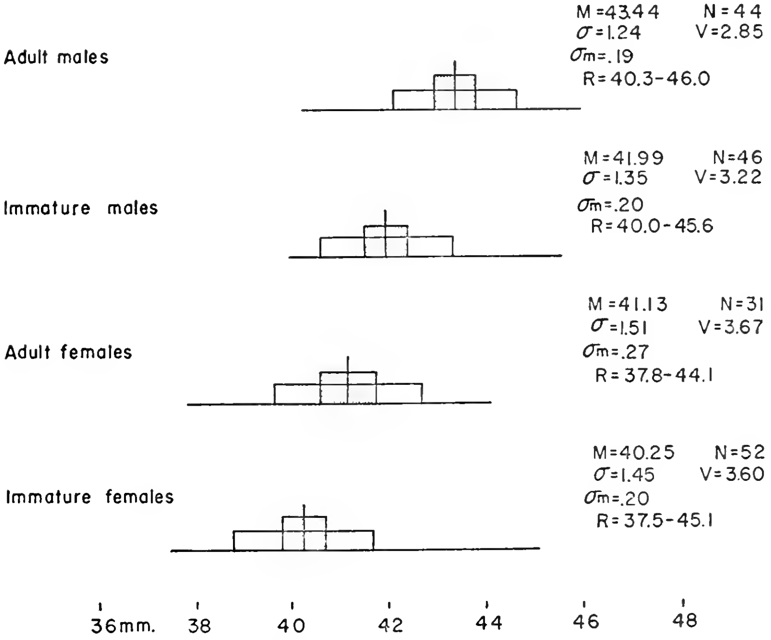
Much along these lines can be learned by examination of large random samples such as that afforded by the Topeka accident. Although only a few species in this sample were measured, the results secured seem to show further the need for segregation of age classes in taxonomic work with some species.

Figure 2 shows the variation in the lengths of wing and tail in the Nashville Warbler. It is evident from the figure that in both of these characters the four sex- and age-classes differ significantly. An accurate idea of geographic variation in this species could not be obtained without separating these classes in comparisons. Age classes in spring and summer, long after the skull is completely ossified, can be segregated only if differences in plumage can be found. In the Nashville Warbler, such differences occur in fall (see annotated list) but these probably are obliterated by the partial prenuptial molt. These facts emphasize the importance, for taxonomic studies, of aged specimens collected in late summer or early fall on their breeding ground and in fresh winter plumage. Figure 3 shows the variation in length of wing in the Lincoln Sparrow in which age seems to be of much less importance than in the Nashville Warbler. Males and females of the Lincoln Sparrow differ significantly in wing-length, but adults and immatures are of nearly the same size. It would seemingly not be necessary to separate age classes in studies of geographic variation in the Lincoln Sparrow. Size data for some other species are given in the annotated list.

WEIGHTS.—Little seems to have been done to determine the correlation of weights with sex- and age-classes. Weight may be the best single index of over-all size and is especially useful to students of the physiology of migration. Weight, however, is subject to the considerable variable imposed by fat condition. In large and comparable series, this variable is probably removed insofar as comparability of means is concerned, but the high variability of weight in most cases naturally results in more overlap (less separability) between populations with means close together than is found with most linear measurements.



Length of wing of 174 *Vermivora ruficapilla*



Length of tail of 173 *Vermivora ruficapilla*

FIG. 2. Statistics of variation in length of wing and tail in the Nashville Warbler. The solid lines represent the observed ranges in millimeters. The stippled boxes represent two standard errors (σm) to each side of the means (vertical lines). The open boxes represent one standard deviation (σ) to each side of the means.

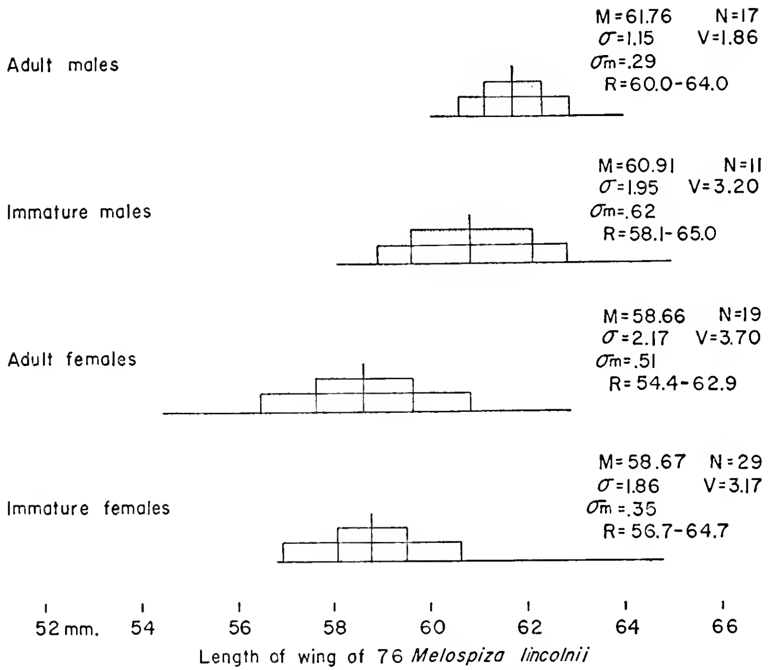


FIG. 3. Statistics of variation in length of wing in the Lincoln Sparrow.

Figures 4-6 show variation in weight in the samples of Nashville Warbler, Mourning Warbler, Yellow-throat, Dickcissel, and Lincoln Sparrow. Each figure is essentially self-explanatory. It will be seen that in the Nashville Warbler and Lincoln Sparrow, weight is roughly proportional to wing-length (shown in figs. 2 and 3), giving about equally good separation of sex- and age-classes in the latter and poorer separation in the former. Data for these and other species indicate a generally greater weight of males than of females, but less difference according to age. In some other species, for example the Yellow-throat, immatures seem to be a little heavier on the average than adults. It is unfortunate that wing-lengths are not at present available for these.

These comments on weight suggest an additional factor which may play a part in rate of migration and which some day may be profitably studied. Suppose that in some species adults and immatures are nearly the same in weight but that immatures have shorter wings. In such a species the immatures are relatively shorter-winged for their weight than adults. In aerodynamic terms,

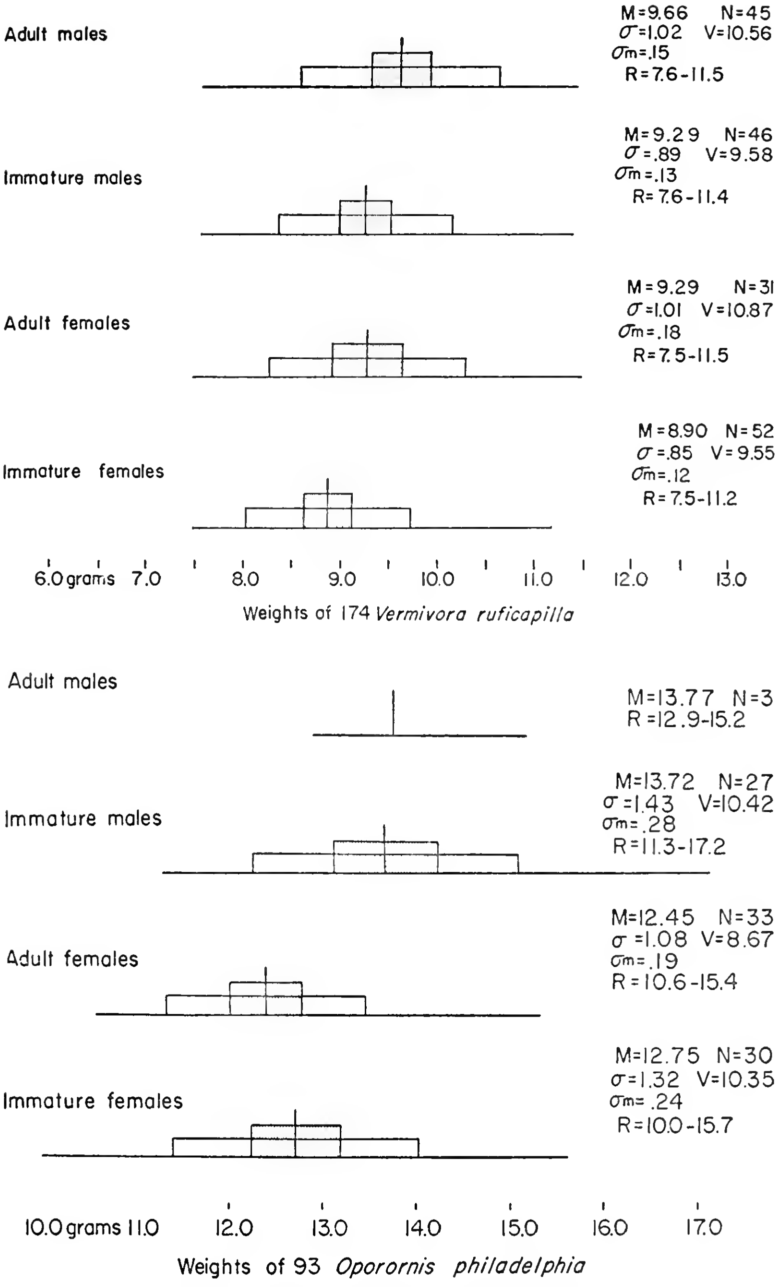
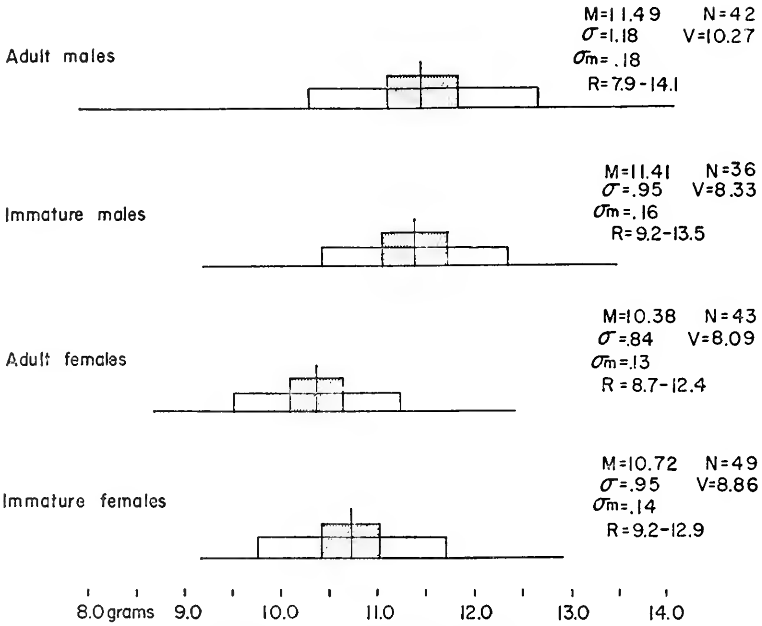
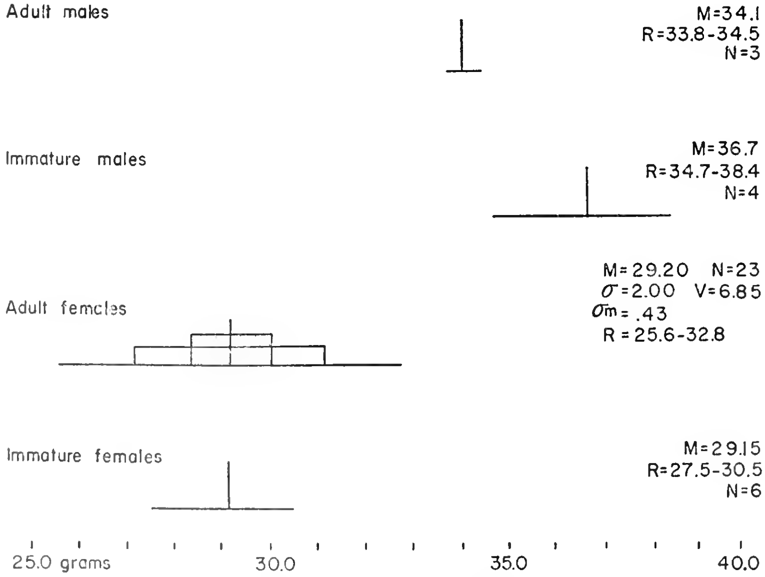


FIG. 4. Statistics of variation in weight in the Nashville Warbler and Mourning Warbler.



Weights of 170 *Geothlypis trichas*



Weights of 32 *Spiza americana*

FIG. 5. Statistics of variation in weight in the Yellow-throat and Dickcissel.

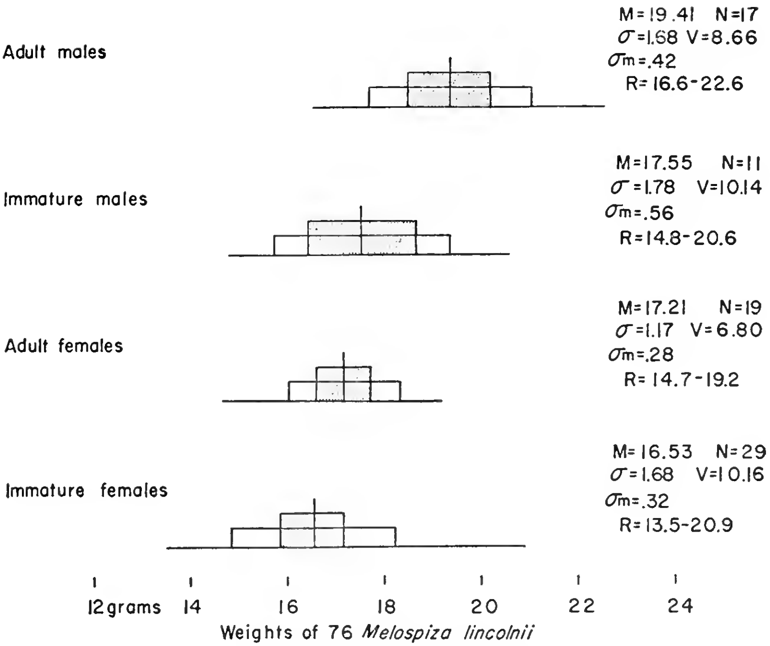


FIG. 6. Statistics of variation in weight in the Lincoln Sparrow.

they would have a higher "wing-loading." (Wing-loading is the result obtained by dividing area of effective wing by total weight; it is here assumed that in a single species wing area is directly proportional to wing length.) This being the case, immatures with higher "wing-loading" would require more energy (derived from fat) to fly the same distance as adults, or with the same amount of fat they would fly a shorter distance. Thus they might tend to be outstripped in migration by adults starting at the same time. The reverse, of course, would also be theoretically true, if adults possessed a higher wing-loading than immatures. Physical factors such as these rather than the differential "virility" postulated by Meinertzhagen (1930:56) might account for the arrival of certain classes of some species on the wintering grounds in advance of others. There are, of course, many other factors which must be taken into account before the effect, if any, of the wing-loading factor can be evaluated. Data for illuminating calculations will become available, however, with the accumulation of abundant information on weights, measurements, and migration patterns.

Computations of Longevity and Survival

Tanner (ms., and letter, April 21, 1955) recently devoted considerable ingenuity to computing by actuarial methods the longevity of the Oven-bird, using the adult-immature ratio in samples killed at a ceilometer at Knoxville, Tennessee. Tanner's computations were based on the simple assumption that

$$\text{S (survival rate)} = \frac{\text{Number of adults in population (or sample)}}{\text{Total size of population (or sample)}}.$$

Further application of such techniques may prove desirable and rewarding. It would seem at present, however, to be a risky procedure, as it has been abundantly shown (see above) that adults and immatures often do not migrate at the same times and rates, and the ratios of adults to immatures in samples of migrants are likely to be far from representative of the true proportions in the populations concerned. It should be added that Tanner is perfectly aware of this objection.

Processing of Samples

Thorough processing of large samples of birds killed accidently is time-consuming. We were fortunate in having considerable assistance; even so, all desirable data could not be obtained from the 1090 birds of the present sample. As aids to others conducting studies of this kind we should mention a few points which may be of assistance.

Birds should be picked up as soon as possible after death, certainly by the end of the day after the accident and preferably much sooner. They should be weighed as soon as possible after collection (weights decrease rapidly, even under refrigeration), and the weights (in grams, to one tenth of a gram) written on tags attached to a leg of each specimen. The sample should then be sorted by species or groups of species of approximately equal size (to avoid crushing of smaller birds by larger ones), placed in boxes, paper bags, or better, air-tight containers clearly marked with date, locality, and other necessary particulars, and relegated to a deep-freeze compartment. For all but the smallest samples, such freezing units are indispensable to complete study. Once frozen, the birds may be selected for study at leisure, but time is still important, as, even when frozen, gonads may eventually deteriorate, and birds eventually become desiccated which is a disadvantage if skins are to be made.

In the cases of large kills, or limited manpower, or both, it may be impossible to process all birds, however desirable this might be. If possible, however, all should be collected, identified, the numbers and species recorded, and rarities saved. Further, partial analysis, or more properly, complete analysis of a partial sample, can be made. Analyses which for any reason require randomness of sample pose a special problem. We think that in very large kills the best way to solve this problem is probably to make one or more transects across the area where dead birds are found. These transects should cross both the areas of greatest and least density (to allow for fast and slow flying species). Their width may be adjusted to give the desired number of birds, that is, the number that can be adequately processed. Another alternative would be to decide to study certain abundant species and pick up all of these. There are other possibilities, but in any event the method of sampling should be thoroughly described wherever all birds have not been processed.

Summary

The foregoing paper discusses accidents in which large numbers of night-migrating birds are killed. A brief historical review of ornithological interest in such occurrences is given, and the types of data provided by the accidents are listed and discussed. In particular, recent accidents occurring in early October, 1954, through much of eastern United States are cited, and detailed analysis is presented of a sample of 1090 birds killed one mile west of Topeka, Shawnee County, Kansas, between September 25 and October 23, 1954.

At Topeka during the period mentioned, 1090 birds representing 61 species were collected and were processed at the University of Kansas. For all specimens, weight, sex, age, and fat condition were recorded, and certain species were measured as well. Some notes on molt were taken. A total of 193 birds was preserved as study skins, and 49 as skeletons. Comments on weight, size, sex, age, subspecific identity, and status in Kansas are presented in an annotated list.

Randomness of this and other similar samples is discussed. A theoretical computation is given for several nights of the numbers

of migrants passing through a plane one mile in width, from 450 to 950 feet above ground level, and oriented to face the arriving migrants. The computed totals give some idea of the tremendous volume of nocturnal migration under some conditions. Potentialities of further study of such events are discussed and a comparison is made with lunar observations.

Differential migration of sex- and age-groups as shown by the larger samples taken at Topeka (Catbird, Red-eyed Vireo, Nashville Warbler, Yellow-throat, Mourning Warbler, Dickcissel, Lincoln Sparrow) is discussed and the history of theories on this subject reviewed. It is shown that age and sex must both be taken into account in studies of differential migration. Several patterns of migration are displayed by the species analyzed, adults migrating earlier than immatures in some instances, young earlier than adults in others, but all seemingly being complicated to varying degrees by differential migration of sexes within age groups. It is suggested that explanations of these patterns may be sought in the life histories of the species involved.

Molt in relation to migration is discussed briefly, and it is held that there is an important relationship between molt and time of migration. Specimens noted to be in molt are listed.

Size differences, in wing length, tail length, and weight are discussed in relation to sex and age, and variation in one or more of these characters is analyzed as found in the Topeka samples of Nashville Warbler, Mourning Warbler, Yellow-throat, Dickcissel, and Lincoln Sparrow. It seems that in some instances significant size differences prevail between adults and immatures and that these age classes should be separated in taxonomic work with species where differences in size are known to exist. When the facts are not known they should be determined, and the large samples collected in accidents to nocturnal migrants present excellent opportunities for ascertaining the facts.

Other uses of material obtained in large migration accidents are discussed, such as computations of longevity and the problems of processing large, accidentally-killed samples. Care should be taken to select samples as nearly random as possible when all birds cannot be processed.

Repeated and thorough analysis of accidental kills should provide a mass of valuable data bearing on many questions and problems which have thus far been little studied.

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26-3856

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Vol. 10, No. 2, pp. 45-75, 6 pls., 1 fig.
December 20, 1956

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UNIVERSITY OF KANSAS
LAWRENCE
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UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

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Published December 20, 1956

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED BY
FERD VOILAND, JR., STATE PRINTER
TOPEKA, KANSAS
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26-4360

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CONTENTS

INTRODUCTION

Taxonomically the Genus *Ammospiza* has received the attention of ornithologists for more than a century. Nevertheless, the behavior of no species of the genus has been studied extensively. The papers of Montagna and Tomkins are the only works that mention behavior and natural history in any detail. There has been an increasing awareness of the importance of ethological data and of their usefulness in systematics. For these reasons, I made a comparative study of the breeding behavior of the Sharp-tailed Sparrow (*Ammospiza caudacuta*) and the Seaside Sparrow (*Ammospiza maritima*) in New Jersey in the spring and summer of 1955.

The Seaside Sparrow is restricted to the Gulf- and Atlantic-coasts of North America, breeding north to Massachusetts. The Sharp-tailed Sparrow breeds south to North Carolina. The overlap of the breeding ranges of the two species is therefore small. Furthermore the forms breeding in the coastal states are restricted to tidal marshes, and the geographically peripheral colonies of each species are small. Irregular nesting is the case for the northernmost colonies of the Seaside Sparrow, on Cape Cod (Griscom, 1944:317), and the same is probably true for the colonies of the Sharp-tailed Sparrow on Pea Island, North Carolina, as indicated by Montagna's failure to locate any breeding birds in July, 1941 (Montagna, 1942b: 256). The center of overlap of the ranges of the two species is in New Jersey where both forms are abundant and can best be studied comparatively.

MATERIALS AND METHODS

The adult sparrows were captured and banded, and sometimes the nestlings were banded. The standard funnel trap, baited with seeds, proved useless for capturing birds of the Genus *Ammospiza*, although migrant Savannah Sparrows (*Passerculus sandwichensis*) readily entered. A Japanese bird net, twenty-five feet long, was used successfully. Eighty-five Sharp-tailed Sparrows and forty Seaside Sparrows were banded at two localities.

All of the adult sparrows were banded with United States Fish and Wildlife Service numbered bands and colored celluloid bands. The colored bands I used were obtained from the Hinton Supply Company of New York City, which manufactures them for cage birds. The firm makes them in seven colors, sold at reasonable prices. With seven colors, the number of combinations, using only one colored band and one aluminum band per bird, is forty-two.

In addition, I dyed many adults and all nestlings. Alcoholic solutions of Victoria Blue B S concentrate and Alizarine Red S concentrate were used. The males were dyed red, the females blue; various areas of the body were colored in order further to individualize the birds. Although the dyes disappeared in less than a month, the markings were helpful on many occasions.

When an adult bird was captured I always sexed it and ordinarily weighed and measured it. The nestlings were weighed and measured daily at intervals of 24 hours. I built a corral of hardware cloth around one Sharp-tailed Sparrow nest in order to measure the young after they left the nest. The sex of any adult was ascertained by examining the cloacal area, as described by Salt (1954:61-75). Sex as determined by this method was corroborated by internal examination of the specimens collected.

A pan balance accurate to one-tenth of a gram was used for weighing. The adults were weighed in a cloth sack, the sack being weighed each time to prevent error owing to variable moisture and other factors.

Dragging the marsh with a rope was ineffectual in finding nests. The birds flushed long before the rope neared them. I found nests of the sparrows by using a blind. From a blind I would determine the approximate location of a nest by watching the movements of the adult birds. Then I would either make a direct search of the vegetation or move the blind closer to find the actual site.

Many hours were spent in blinds. I had two in operation throughout the breeding season, and it was from these that most of the data on behavior were accumulated. Observations were made by means of a 7 x 50 coated binocular and on occasions by means of a 19.6x spotting telescope.

DESCRIPTION OF THE AREA

The intensive work was carried out on the marshes west of the town of Lavallette in Ocean County, New Jersey. Further observations were made at other localities in the county, in particular at the Chadwick marshes (plate 6), one mile north of the Lavallette site, where many of the Ammospizas were banded. The breeding Ammospizas of the localities are the nominate races, *A. c. caudacuta* (Gmelin) and *A. m. maritima* (Wilson).

Characteristic of the sand beaches of the Atlantic coast of the United States are offshore bars which, when exposed, form long bays parallel to the coastline. These bays become surrounded by marshes that in turn are inhabited by the two species of *Ammospiza*. The birds prefer the marshes closest to the ocean (plate 6). I made trips to the marshes on the mainland side of upper Barnegat Bay and found only a few Sharp-tailed Sparrows and no Seaside Sparrows in residence.

The island of the Lavallette marshes that I worked on was approximately 1400 feet long and 600 feet wide. One-third of the east central end of the island was covered with sand fill, pumped there several years before the study was begun (plate 1, fig. b). The island was also ditched. The four east-west ditches are spaced 125 feet apart; the two ditches perpendicular to these are 340 feet apart and are situated in the western portion of the island. These ditches, originally dug as a means of decreasing the mosquito population, are one foot wide and almost three feet deep. The excavated earth is deposited in a row paralleling the ditch. The entire island, excluding the sand fill is not more than two feet above normal high tide. In August, 1955, abnormally high water, a result of hurricane "Connie", rose four to five feet and covered all but the tops of the bushes and a few mounds of sand. Low tides expose no mud flats for the edges of the marsh are nearly vertical banks and the water along the edges is more than one foot deep.

The average temperature for July, compiled over a 34 year period at the Asbury Park weather station is 72.6°F. The average precipitation from May through August, acquired over the same length of time, is between 3.5 and 4.5 inches per month.

In spring and summer the prevailing winds are from the south and southwest. Therefore, the south and west shores of the island are subject to greater inundations by water. The fact that the island is unprotected by neighboring islands from the open expanse of the bay on this side is also of importance in this respect. The north and east shores, on the lee side of the island, are guarded from the open bay by nearby land. The exposed southern shores, where there was open mud and sparse patches of cord-grass, were the preferred feeding areas of the Seaside Sparrows. Lack of exposed and open feeding areas may account for the absence of this species in areas that otherwise seem to fulfill the requirements of the species.

Two major drift lines were present on the island: one within a few feet of the waterline consisted mostly of dead eel grass (*Zostera marina*), and the other, situated close to the cattail strip, contained a variety of flotsam (pl. 2, fig. a).

FLORA

The vegetation on the island consisted chiefly of smooth cord-grass (*Spartina alterniflora*), black grass (*Juncus gerardi*), cattail (*Typha* sp.), and marsh-elder (*Iva frutescens*). Other plants identified on the area were: common reed grass (*Phragmites communis*) and slender grass wort (*Salicornia europea*). Black grass grows on the inner, dryer portions of the marsh, and cord-grass prefers the wetter portions, growing to the edge of the water. The marsh-elder bushes mostly are restricted to the mounds of earth dug from the ditches. Cattails, in general, grow in a narrow band paralleling, but back a few yards from, the shoreline. Areas of mixed black grass and cord-grass occurred.

REPTILES

Diamond-backed terrapins (*Malaclemys terrapin*) were the only reptiles recorded from the study island. Several were taken on land, but the majority were seen in the waters about the marsh.

On June 27 a black snake (*Coluber constrictor*) was seen in a bushy area bordering a marsh on the mainland side of Barnegat Bay. A few Sharp-tailed Sparrows were seen in the same locality and a singing male (G. E. W. 559) with testes 14 x 8 mm. and a female (G. E. W. 558) with a brood patch were collected.

MAMMALS

Only two species of mammals, both abundant, were present on the study island: the meadow vole (*Microtus pennsylvanicus*) and the muskrat (*Ondatra zibethicus*). The muskrats dug burrows beneath the level of the water into the banks of the island, used the ditches as routes to the interior of the marsh and built some small houses, mostly from cattail stems.

PREDATORS

Unless the above named mammals preyed on the sparrows, all of the enemies of the colony at Lavallette were avian. Both Crows (*Corvus brachyrhynchos*) and Fish Crows (*Corvus ossifragus*) visited the local marshes frequently as did a

Marsh Hawk (*Circus cyaneus*). I watched the Marsh Hawk make many passes at what I thought were sparrows, but the only animal I ever saw caught by the hawk was a *Microtus*. The sparrows were alarmed when the hawk appeared, quickly and silently disappearing into the grass.

At least two nests on the Lavallette Marsh were destroyed by predators in the course of the breeding season of 1955. One nest of the Seaside Sparrow was empty when I checked it on July 3; on July 2 it had contained four young, three days old. On July 21 I found a dead Sharp-tailed Sparrow, approximately three days old, lying on a patch of matted grass. A hole was in the flank of the bird and blood was present about the bill. This nestling was not from a nest under observation.

PASSERINE ASSOCIATES

On the Lavallette marshes the only passerine associates of the two species of *Ammospiza* were Song Sparrows (*Melospiza melodia atlantica*) and Long-billed Marsh Wrens (*Telmatodytes palustris palustris*). Two pairs of Song Sparrows and less than six pairs of marsh wrens nested on the study area. One Song Sparrow nest was found and is plotted on the map (pl. 1, fig. b); the other pair nested somewhere along the east shore of the island. The Song Sparrows at the east end of the island obtained most of their food from the grounds of the Lavallette Yacht Club across fifty yards of water to the east. The pair that nested in the western portion of the island fed along the sand fill or along the bases of the marsh-elder. Their nest was built in the most extensive area of these bushes; it was placed approximately one foot above the ground in a small dead bush and gained support and concealment from the surrounding black grass. Three of the four eggs hatched on June 30, and the young left the nest on July 11. Both parents fed the offspring.

The marsh wrens fed and nested in the cattails. I never saw these wrens away from the cattails.

WINTER STATUS AND SPRING MIGRATION

Ocean County is ten miles south of the area treated in Cruickshank's regional work (1942). He considers both species as rare to casual winter residents. Concerning the spring migration of the Sharp-tailed Sparrow he says (p. 456) "The first widespread wave never comes before April 25, however, and most of the birds arrive in May." He mentions that late May is the height of migration and that stragglers are passing through up to the middle of June. The arrival of the Seaside Sparrow in spring is similar (p. 458): the first widespread movement is in early May, the peak is reached in the third week of the month, and stragglers have been recorded through the second week in June.

I was in the field in Ocean County almost daily all spring and found no Seaside Sparrows and only two Sharp-tailed Sparrows north of Barnegat Inlet, Ocean County, before May 5. I waded through the marshes at Chadwick, Lavallette, and Island Beach State Park on April 27 when high tides covered all of the dense vegetation and saw no sparrows of the Genus *Ammospiza*. If many had been present on this date I would have seen them. On May 5 both species were plentiful on the Chadwick marshes. Furthermore, the Seaside Sparrows were defending territories. The absence of the two species the previous day indicates a large nocturnal flight.

It was during the second and third weeks in May that the sparrows of this genus were most abundant. In this period many unbanded Seaside Sparrows were in the patches of cattails that were being defended by the resident males from other territory-holders.

One *Ammospiza caudacuta subvirgata* (G. E. W. 545) was taken in the course of the study. It was a female (ovary: 7 x 5 mm.) weighing 15.3 grams ("moderate fat"), taken on June 8, 1955, on a marsh near the mouth of the Manasquan River on the Monmouth-Ocean County line. This marsh is decidedly less brackish than the Lavallette and Chadwick marshes. The specimen was the only *Ammospiza* seen there and was probably a migrant, despite the late date; this subspecies is known to occur late along the Atlantic Coast south of its breeding range. Cruickshank (1942:454-455) considers the peak of spring migration for this subspecies to be reached in late May.

To find *A. c. subvirgata* in a marsh seemingly not saline enough for the nominate race is not surprising. *A. c. subvirgata* breeds in marshes, along the coast of New England, which are almost fresh water (Montagna, 1942b:256). *A. c. caudacuta* is only casual away from salt water.

TERRITORY

In a general treatise on the subject of territorialism, Nice (1933: 98), summarizing Howard, stated: "Territory implies in the male bird isolation, advertisement, fixation, and intolerance." I concluded from my observations that all four requirements are exhibited by male Seaside Sparrows while none of them is well developed in male Sharp-tailed Sparrows. This subject is discussed separately for the two species.

Tomkins (1941:38-51) studied populations of *Ammospiza maritima macgillivrayii* near the mouth of the Savannah River in South Carolina and Georgia and concluded that this form is not territorial. In support of his conclusions, he quoted Nice (1933:90-91) as follows: "Territory cannot mean just the nest spot when the adults feed in common; this may be 'nest territory,' but it is a very different matter from a territory in its strict sense to which parents confine themselves during the breeding season. Again, the very essence of a territory lies in its exclusiveness; if a bird's range is not defended, it is not a territory."

The feeding and nesting grounds of breeding Seaside Sparrows are often separated by a portion of the marsh which is not used by the birds. This complicates study of the territorial habits of the species. It does not mean, however, that the species is not territorial.

The birds studied by Tomkins had separate feeding and nesting grounds. Concerning this, Tomkins (1941:43) states that "The Seaside Sparrows of this locality [Savannah River area] often live where the two requirements [adequate feeding grounds and suitable nesting cover] are not always together or even meeting, but also where the feeding grounds and the nesting place are separated by a short distance."

Six of the eight original pairs of breeding Seaside Sparrows of the Lavallette colony fed in areas separate from those in which they nested. I found the eight nests of the original residents and banded and dyed all of the adults. The owners of two nests did not have separate nesting and feeding areas. One nest was built within fifteen feet of the south shore of the island, adjacent to the feeding area. The other was built within a few feet of the north shore. The female of this nest obtained food along the shore in the immediate vicinity of the nest. Her mate was absent; in all probability it was the singing male which I took from a nearby bush, before I found it advantageous to use the island as a study area.

The remaining six pairs flew to the south or west shores of the island in order to feed. None of these six nests was more than 100 yards from the feeding grounds (pl. 1, fig. b).

It was comparatively easy to see that the males defended an area surrounding the nest. It was more difficult to see that the pairs fed on separate plots of shoreline, each defended by the male, but I am convinced that this was the case.

The nest area was defended by the males through singing and chasing. I saw no instances of a female entering into territorial disputes; nevertheless, I did see a female chase a Sharp-tailed Sparrow away from the vicinity of her nest.

Tomkins (1941:46) did not consider the song of *A. m. macgillivrayii* to be "a declaration warning other birds away." After observing the behavior of males of *A. m. maritima* I am convinced that advertisement of intolerance is the primary purpose of song in this species. An account of the activities of a male Seaside Sparrow on May 6 on the marsh at Chadwick demonstrates this point. In an hour (6:01-7:01 a.m.) the bird sang 395 times, an average of 6.6 times per minute. He faced his nearest singing competitor when singing, which in the course of this hour was usually a male approximately 250 feet away across a creek. The two competitors almost always alternated their songs and frequently the singing of one seemed to stimulate the other bird to sing. Although the song of the Seaside Sparrow is short and unmusical it is loud, especially when compared with the song of the Sharp-tailed Sparrow. Elevated perches such as the tallest cattail stems or isolated bushes were used as singing and observation perches.

The chase of the Seaside Sparrow is not vigorous, but in all cases the intruder was seen to give way to the defender. I saw no physical fights between Seaside Sparrows. Chase by a defending bird was close to the ground and directly toward the intruder. Sometimes the attacking male emitted chipping notes when first sighting or flying towards his adversary.

In the hour of observation mentioned above, no other Seaside Sparrows entered the bird's territory, which consisted of a strip of cattail and shoreline, 250 feet long and no more than 25 feet wide. At other times Seaside Sparrows did enter this male's territory, and he drove them out as soon as he saw them. Savannah and Swamp Sparrows, which for a few weeks migrated through the area, were not chased, but Sharp-tailed Sparrows were chased at times.

Several times I flushed a particular male Seaside Sparrow from the northwest tip of the Lavallette study island so that it flew to the island to the north. Seaside Sparrows of this north island immediately made themselves conspicuous by chipping and then drove the non-resident individual back to its own territory.

The first time I heard what is described below as the social call of the Seaside Sparrow was on June 30 when an unbanded sparrow alighted in a marsh-elder bush near a nest. The individual called twice as it came near. The sound immediately aroused the owners of the nest and the male flew directly toward the strange bird. The intruder quickly and silently flew away.

My field notes refer to many other instances of territorial defense of the nesting area; it seems superfluous to cite them here.

Additional proof of territorialism in Seaside Sparrows was obtained by identifying and plotting the location of all the marked individuals, which I saw each day while systematically traversing all the available habitat on the island. Surprisingly, I did not once record a resident Seaside Sparrow in what I considered another male's territory in the month and a half (June 15-August 1) that I worked on the island at Lavallette.

The fact that the adult Seaside Sparrows did not search for food communally, or that different pairs did not utilize one particular area at different times was most apparent when the pairs were feeding young. From the blinds I first noted that the adults from any given nesting territory always flew in the same direction towards the shore. After moving a blind closer to the shore I noted that once an adult arrived at the open or sparsely vegetated shoreline, that adult restricted itself to a certain portion of the shoreline. These shoreline territories were plotted on field maps and appear on the map in plate 1, figure b. One method used to ascertain the boundaries of these shoreline feeding territories was a census taken from a boat. Many times I circled the island in a skiff identifying the marked sparrows as they appeared along the shore. The feeding sparrows were always found in the same areas around the island. Straight lines can be drawn between the nest sites and feeding areas of each pair of Seaside Sparrows without having any lines cross (pl. 1, fig. b). These lines correspond to the flyways used by each pair to go to and return from the feeding area. I consider the area defended about the nest, the segment of shoreline used by a pair of Seaside Sparrows and the connecting flyway to constitute the territory of a male Seaside Sparrow. If the flyways of any of the pairs had crossed, a situation of mutual exclusiveness would not have existed and a territory could not have been defined for the species.

It is generally agreed that territorial species engage in a minimum of fighting. Song and display have been evolved to substitute for actual combat which demands a greater amount of energy. Additionally, the mere presence of an individual in an area previously established as its territory probably serves to keep birds of nearby territories away. I think that male Seaside Sparrows defend the feeding area and flyway as a part of their territory by advertisement through use of these areas. The birds at Lavallette rarely sang on the feeding grounds and I noted only a few chases originating there. The sparrows rarely landed along the flyways. The constant use of these areas probably served as territorial defense, however. This supposition is supported by the fact that feeding areas and flyways of different pairs were mutually exclusive.

Nice (1941:457) divided territory into six categories. Type A (mating, nesting, and feeding ground for young) is the type exhibited by the Seaside Sparrow. The territory of a male Seaside

Sparrow must contain an area of open mud and/or sparse vegetation where food can be obtained and also enough suitable cover to conceal the nest. I suspect in the case of the few males studied on the marshes at Chadwick that the territories the males established (strips of cattails and adjacent shoreline) did not have suitable nesting cover, because these males were unmated on June 15 when I left this study area because of human interference. Suitable nesting cover and feeding areas were separated by short distances of unusable marsh for most of the sparrows on the Lavallette study area. This fact caused the adults to commute from one site to the other. Photographs of shoreline habitat suitable for feeding by Seaside Sparrows appear in plate 2.

The area defended about the nest tended to follow the rows of marsh-elder bushes (pl. 3, fig. a), probably because these bushes supplied suitable song and observation perches. The segments of shoreline used by each pair were less than 75 yards in length and scarcely 20 feet wide. I never recorded Seaside Sparrows foraging in the interior of the marsh.

Sharp-tailed Sparrows were more abundant than Seaside Sparrows on the marshes at Chadwick and Lavallette. Sharp-tailed Sparrows were the more difficult to net because of the peculiar organization of the colonies. This organization, described below, also made nests of that species the more difficult to find. Only intensive netting at both localities produced enough marked individuals for me to study the breeding behavior of the species.

At Chadwick, where I netted most of the 85 Sharp-tailed Sparrows that I banded, my efforts were concentrated on one segment of the marsh. Marking made it evident that the males were not territorial, although they did confine themselves to what might appropriately be called a breeding home range, the area to which an individual confines itself in the course of one nesting attempt. Observations of marked birds also indicated that there was considerable overlap of the breeding home ranges of individual males.

I recorded a few marked Sharp-tailed Sparrows often enough and over a long enough period (more than one month) to gain a good idea of the size of the breeding home range of the males, which I estimate to be three to four acres. This estimate was made at Chadwick, where large areas of suitable uniform habitat occur. Females are more secretive than males, but seem to restrict themselves to areas considerably smaller than those of the males. My observations of two females that were feeding young indicated that each female restricted herself to an area of less than one acre. Female

Sharp-tailed Sparrows possibly are territorial, although I recorded no disputes that would substantiate this possibility.

If I am correct in my estimates of size of breeding home range in Sharp-tailed Sparrows (males, three to four acres; females, approximately one acre), certain observations made by Montagna and me are readily explainable.

My netting operations indicated a surplus of male Sharp-tailed Sparrows in a given area. At Chadwick, I netted as many Sharp-tailed Sparrows as I could, without regard to sex. Here I captured 39 males and 16 females (six individuals remained unsexed). On the Lavallette study island, netting was more selective; here I attempted to net the females of the nests I found. The sex ratio at Lavallette was 15 males to eight females (one juvenile was not sexed). Three of the eight females were netted at their nests.

Montagna (1940:196) decided from collecting and observations that male Sharp-tailed Sparrows either outnumbered the females or were polygamous. The results I obtained from netting seemed to indicate a surplus of males. Banding, however, showed that in the breeding season males range over a larger area than do females. With this knowledge, the discrepancy between the number of males and females captured is explainable without an unbalanced sex ratio. If the males range over an area four times as large as that of the females, theoretically, four times as many males should be caught at every placement of the net provided the net remained in place long enough to capture all the birds using the area. In practice, this is essentially what occurred.

Other behaviorisms of this species indicate that it is not territorial. The song of the male is not loud and does not seem to be an advertisement to other birds. In fact, the song of this species is so quiet and lengthy when compared to that of the Seaside Sparrow that I at first thought I was hearing "whisper" or "practice" songs. These qualities of the song seem to indicate that the "advertising" function of song of territorial species is lacking or unimportant in Sharp-tailed Sparrows.

I suspect that male Sharp-tailed Sparrows do not even know where nests are. On July 18 at 7:00 a. m. I was watching a nest from a nearby blind when an unbanded male (I saw the individual sing later) appeared. As the bird foraged through the black grass, it headed directly toward the nest. When the male was almost one foot from the nest the incubating female left. She ran from the tussock and flew a short distance away to a cattail stem. From here she watched the male, which seemingly oblivious continued foraging, coming within inches of the nest. As the male walked away from the nest the female returned. At 8:00 p. m. the same day I was in the blind again. The female was out searching for food when a different, banded male appeared. In his foraging, the male walked up on the grass stems over the nest. The male apparently saw the young (two had hatched on July 17 and one on July 18) for he turned his head and seemed to peer down under the stems. The female appeared (with food) as he was doing this; she flew directly toward him and he flew away. The male was not seen near the nest in later observations.

On July 1 (6:50 a. m.) I was in a blind near another nest as the female approached with food for the young. At this moment a male appeared and the female immediately flew away. The male perched on a tussock within two feet of the nest, sang, and then flew off. The female reappeared in a few seconds without the food. She searched through a clump of black grass four feet from the nest, caught a small, pale green insect, fed it to her one young (there were also two eggs in the nest) and began brooding.

VOICE

Song

Only males of the two species sing. The normal song of the Seaside Sparrow lasts just under two seconds, the buzzing final note constituting three-quarters of the song. Saunders (1951:257-258) describes this song as short, and buzzlike, beginning with two or three short, rather faint notes and ending in a trill at first loud but fading away toward the end. The introductory notes are followed by a higher-pitched, loud, strongly accented, but buzzy note. This note is usually higher than the final trill and connected with it. The song has been written as *tup tup ZEE reeeeeeeeee* and *tup TEE tle reeeeeeeeeee* (Saunders, 1951:257), *cutcut, zhé-eeeeeeeee* (Peterson, 1947:232) and *che-zheéeege, che-zhée, che-wéege, chur-zhée* and *too-szheée* (Stone, 1937:910). My field notes contain the following: *CHUR-er eeeee, CHUR eeeeee* and *oka-CHE weeeee.* These variations in the phonetic representation of the songs are attributable mostly to the birds. Not only is there variation among individuals, but also individuals vary their songs. Birds that I heard giving a characteristic song suddenly sang a different type for awhile, and then reverted to the original. The bill is elevated and opens considerably with each note; the head bobs with the loud note. Typical singing postures are shown by Tomkins (1941: pl. 3).

The song of the Sharp-tailed Sparrow, as described by Saunders

(1951:256-257), is short and insectlike, introduced by one or two short notes; the remainder is a somewhat wheezy trill, growing fainter towards the end. Sometimes there are two trills on different pitches, and occasionally a final short, low note. The quality is as though the sound *sh* ran through all but the introductory notes. Saunders writes these trills as: *tsup tsup shreeeeeeeee* and *tip tish eeeeee shaaaaaaay*. The bill is opened slightly with each note, as I saw when I watched a singing bird with the sun directly behind it. Montagna (1942a:116) noted that *A. c. caudacuta* sang less often than the more northern *A. c. subvirgata*.

Both species have specialized flight songs, but in the birds that I studied these songs were infrequent and seemingly unimportant. The flight song of the Seaside Sparrows consisted of a double version of the normal song. Although I heard it only a few times, the flight song of the Sharp-tailed Sparrow seemed slightly louder than the normal song. This song is given by both species as the bird flutters upward ten or 20 feet and glides back down.

Singing begins at daylight and decreases at 9 or 10:00 a. m. when the temperature rises. On cloudy days singing seemed to last longer. Towards dusk singing again increases, but not to the frequency of the morning peak.

The major differences between the songs of the two species are in loudness, length, and frequency. The fact that the Seaside Sparrow sings louder than the Sharp-tailed Sparrow is mentioned by Stone (1937:906). On windless days I heard singing Seaside Sparrows more than 200 yards away; Sharp-tailed Sparrows were inaudible at distances of more than 40 yards. The song of a Seaside Sparrow is rarely longer than two seconds; the song of a Sharp-tailed Sparrow usually lasts for almost 20 seconds and consists of a variable number of phrases like those described by Saunders. A Seaside Sparrow that I watched for one hour sang 395 times or 6.6 times per minute. I doubt that any of the Sharp-tailed Sparrows sang more than 20 times per hour, although I made no comparable count.

Additionally, Seaside Sparrows sing from exposed perches such as tall cattail stems and tall or isolated marsh-elder bushes. Sharp-tailed Sparrows do not often use conspicuous perches for singing. They sing while on the ground or when in flight. They do use exposed perches as observation posts and occasionally sing from them.

Seaside Sparrows often face their nearest neighbor when singing and alternate songs with this bird. The one time Sharp-tailed

Sparrows almost always sing is when they are involved in fighting. In such a case the several birds sing simultaneously.

Seaside Sparrows began singing the morning after their nocturnal arrival. For resident birds, singing is at its maximum at this time and is maintained at a high level throughout incubation. At hatching of the eggs, singing declines sharply; males then are busy aiding in care of the young. Males that have successfully reared a brood rarely sing after the young leave the nest.

Sharp-tailed Sparrows sang infrequently when they first arrived, and singing did not reach its peak until late May. By August singing had almost ceased in this species.

Song of the Seaside Sparrow functions importantly in the establishment and maintenance of its territory. Newly-arrived males sing vigorously. In the Sharp-tailed Sparrow I think song is merely an expression of sexual excitement because song does not reach maximum frequency until the females arrive and become receptive to the males.

Differences in song correspond to differences in territorial behavior. The distinct, loud song, sung often and from exposed perches, which is frequently alternated with that of the nearest competitor, is given by the Seaside Sparrow, a territorial species. The indistinct, quiet song, sung infrequently and often from unexposed places belongs to the Sharp-tailed Sparrow, a non-territorial species.

Calls

Seaside Sparrows give a soft, lisping call note, probably the one referred to by Saunders as a squeaky *tseep* (1951:258), that functions as a social call. When migrants were numerous on the marshes at Chadwick I heard this note often. At Lavallette I did not hear it until June 30 (work began there on June 16) and then it was from an unbanded, non-resident bird. In late July and in August the number of non-resident sparrows increased and the social call was heard often. I never heard a resident bird give this call. On December 29, 1955, on a marsh at the mouth of the Manasquan River on the Monmouth-Ocean County line, a group of wintering Seaside Sparrows frequently used this call. I do not know whether the Sharp-tailed Sparrow has a comparable call.

Both species emit alarm notes. Although variable, the Seaside Sparrow has two general types. One, recorded by me as a short *chip* or *tick* was given by both sexes whenever I was near a nest. The other type, a high, sharp *tsip*, is indicative of a higher degree of

PLATE 1

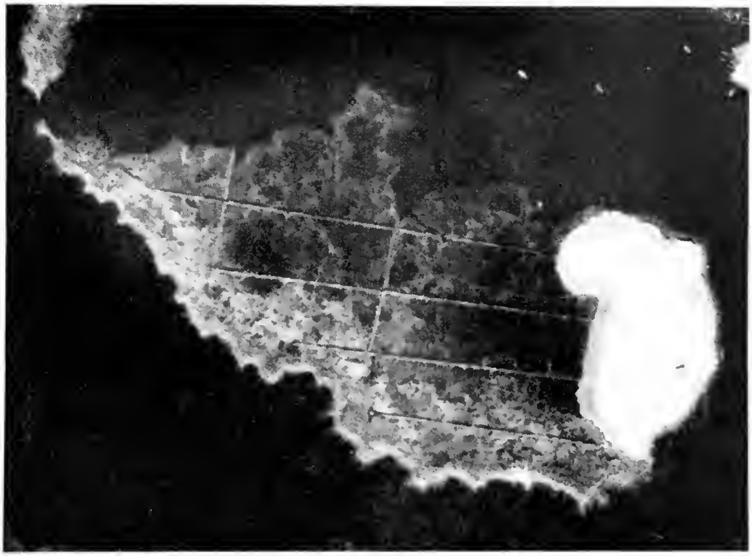


Fig. *a*. An aerial photograph of the Lavallette study island. One inch equals approximately 375 feet. The area covered by sand has been extended since this photograph was taken. This is indicated in figure *b* of this plate.

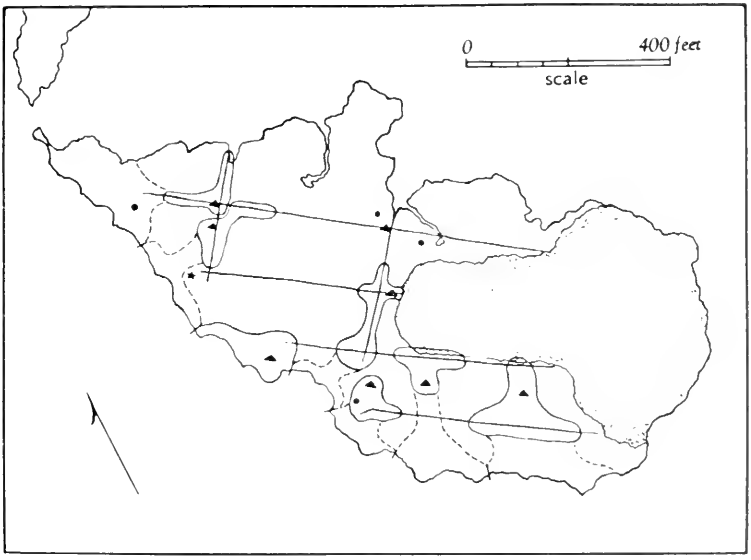


Fig. *b*. Map of the Lavallette study island. All fringillid nests that I found are indicated and the territorial boundaries of the Seaside Sparrows are shown.

▲—Seaside Sparrow
•—Sharp-tailed Sparrow
★—Song Sparrow

PLATE 2

FIG. *a.* The south shore of the Lavallette study island showing the two major driftlines and the sparsely vegetated areas. This is the feeding habitat of the Seaside Sparrow.

FIG. *b.* A close-up view of a segment of the shoreline. Note the spacing of the clumps of cord-grass (*Spartina alterniflora*). A six inch ruler propped against a 12 inch stick is included to indicate the size and spacing of the plants.

PLATE 3

Fig. *a*. The inner portion of the marsh on the Lavallette study island showing the rows of marsh-elder bushes (*Iva frutescens*) and the extensive areas of black grass (*Juncus gerardi*). Areas of mixed black grass and cord-grass appear in the foreground. All the nests of Sharp-tailed Sparrows were found in the areas of black grass. Four of the eight nests of Seaside Sparrows were in the marsh-elder. One of the blinds that I used is shown in this photograph.

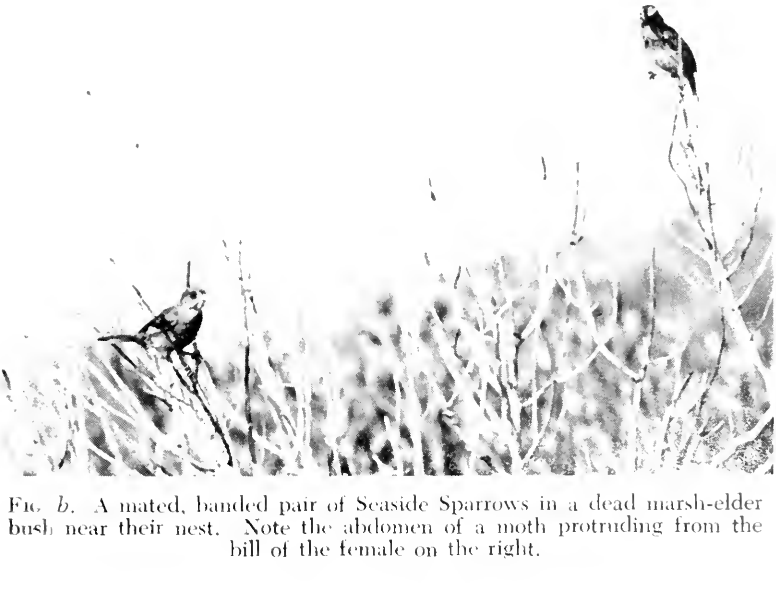


Fig. *b*. A mated, banded pair of Seaside Sparrows in a dead marsh-elder bush near their nest. Note the abdomen of a moth protruding from the bill of the female on the right.

PLATE 4

Fig. *a*. A female Sharp-tailed Sparrow at the entrance to her nest. The throat on this bird is dark because of dye applied by me.

Fig. *b*. The nest of a Sharp-tailed Sparrow viewed from above. Stems of black grass were parted to take the picture. The outer rim of this nest (lower right) is made of living stems of black grass.

excitement. When I captured young already out of the nest, or when I investigated nests containing young old enough to depart, the adults gave this call. The tail is jerked downward each time this note is given.

The alarm call of the Sharp-tailed Sparrow is not so loud as that of the Seaside Sparrow and it is not given so often. I described it as a short *tsick* or *tsuck.* Females emitted such calls when I was at their nests or when male Sharp-tailed Sparrows came near their nests. Males may have a similar call, but I never recorded it. Montagna (1942a:116) remarks on the quietness of this species. This is especially evident when one compares Sharp-tailed Sparrows with Seaside Sparrows.

COPULATION

In late June at the Lavallette area there was an influx of unbanded Seaside Sparrows. Certain of these new arrivals established territories in areas unoccupied by the remaining original residents. These new residents were birds that probably had unsuccessful nestings elsewhere. Because of tropical storms that almost covered the island with water in August, I doubt that any of these late nestings were successful. On July 7 at 8:30 a. m., while watching a pair of these new arrivals, I recorded my only observation of copulation in the Seaside Sparrow. The female seemed to be searching for a nest site when copulation occurred. The female crawled about in a marsh-elder bush seemingly testing the various forks in the branches for size. The male followed her, remaining a few inches above and behind. Several times the two birds disappeared in the lower branches and were hidden by the surrounding black grass. Finally, while the female squatted on a branch the male mounted. He fluttered his wings before mounting and continued to do so as coition took place.

I began observations at Lavalette on June 16, too late to observe copulation of the early residents. All the nests contained eggs by that time. At Chadwick, pair formation seemingly never occurred, at least with the males I was studying. The territories established by males at Chadwick contained few marsh-elder bushes. Possibly females, finding no suitable nest sites, refused to accept these territories.

Copulation in the Sharp-tailed Sparrow was observed several times. It occurs most frequently in the course of, or immediately following, a fight between several males. I do not know what instigates the gathering of several males into these groups; it may be a certain behaviorism of a female, or possibly, merely the appearance of a female. Montagna (1942a:117) was convinced that females of *A. c. subvirgata* were present in these fights. On the other hand, in two instances with *A. c. diversa* where he collected all the birds in the group, no females were present. Twice, at Chadwick, my observations indicated that females of *A. c. caudacuta* were not always involved in these groups. In these instances all the birds in the group had previously been banded and diagnosed as males. Possibly a female was the original stimulus of these groups, and she may have disappeared while the males were fighting with each other. I found it difficult to distinguish fighting males from a copulating pair. On June 3, however, a banded pair was observed. Copulation occurred on the ground. The male fluttered his wings as he mounted and the female remained motionless. Copulation lasted approximately three seconds; immediately thereafter the male flew to a nearby cattail stem and the female climbed a tussock of grass and chipped quietly. This same female was seen to copulate with other males, and males were observed copulating with several females.

A. m. maritima is monogamous, the pair-bond being maintained throughout a breeding cycle. *A. c. caudacuta* is promiscuous, relations between the sexes being limited to copulation. For *A. c. subvirgata* a relationship other than promiscuity has been intimated (Lewis, 1920:587-589). Concerning observations of the nest he found at Yarmouth, Nova Scotia, Lewis wrote: "The nest was found after I had quietly watched the parent Sparrows for about an hour, while they were bringing food to their young. . . . The male sang from time to time from a piece of driftwood on the marsh about 30 feet distant from the nest. When I was examining the nest and the young birds, the parents made no demonstration for some minutes, but later they came near and uttered chip's, much like those of Savannah Sparrows."

NESTS

I found the nests of all eight pairs of Seaside Sparrows which nested on the Lavallette study island in 1955. Four nests were supported by marsh-elder bushes, three of which were dead. These nests were placed low enough to be hidden by numerous stems of black grass, as were the other four nests. Of the remaining four nests, three were placed in tussocks of black grass and the fourth one gained support mostly from cord-grass stems. The eight nests ranged from 9 to 11 inches (9.6 inch average) from the rim to the ground, the four nests in the bushes being the highest. The outside diameters of the nests ranged from 3 to 4.5 inches (3.9 inch average) and the outside depth varied between 2 and 3.5 inches (2.7 inch average). Seven of the nests had an inside depth of 1.5 inches; the other one was only an inch from the rim to the floor. The inside diameter of the cup varied between 2 and 2.5 inches.

As mentioned above all eight nests were shielded by stems of black grass. Stems were not woven over the nests by the birds; rather it was the choice of the nest sites that resulted in the concealment. The only plant used for nest material was black grass.

In all cases the black grass limited the directions from which the nests could be entered. Six of the nests were approached from a direction varying between northeast and southeast. The prevailing winds of spring and summer are from the south and southwest; the black grass consequently leans in the opposite direction. The remaining two nests were entered from the northwest. These were nests built in marsh-elder bushes where the grass stems were held upright by the branches of the bushes.

One nest, built in a small dead marsh-elder bush, was tilted by the growth of stems of black grass which were used for support on one side. This tilting did not cause the contents to spill, but, I judged, did cause the adults to desert the nest.

Seven nests of the Sharp-tailed Sparrow were found; two of these were old nests. Four of the five nests used in the breeding season of 1955 were found on the Lavallette marsh study area, the other one I discovered on the Chadwick marshes. Two young Sharp-tailed Sparrows that I saw at Lavallette were not from nests I found, nor were they from the same nest. Therefore, a minimum of six Sharp-tailed Sparrows bred on the Lavallette island. Measurements were taken of only the five nests that were used in 1955. The Sharp-tailed Sparrow builds its nest closer to the ground than does the Seaside Sparrow. The five nests were five to six inches off the ground; the two nests of a previous year appeared to have been no higher. The Sharp-tailed Sparrow nests were built in areas where black grass was the predominant plant, and the nests were constructed entirely from this grass. The outside diameters varied from 3 to 4.25 inches (3.4 inch average). The outside depth of the nests varied from 2 to 3.5 inches (2.8 inch average). The inside depth was 1.5 inches in all nests and the inside diameter ranged from 2 to 2.5 inches (2.1 inch average).

Harrison F. Lewis (1920:587) studied a nest of *A. c. subvirgata* in a small salt marsh near Bunker's Island at the southern end of Yarmouth Harbor, Yarmouth, Nova Scotia, which he found on June 12, 1920. For details of this nest I quote Dr. Lewis. "The nest proper was a neat, round cup of fine, dry, dead grass, with some horsehair in the lining. Its foundation consisted of some small masses of 'eel-grass' and roots. Its dimensions were: inside diameter, 2.5 in.; outside diameter, 4.5 in.; inside depth, 1.5 in.; outside depth 2.375 in. It was elevated above the general surface of the marsh by being placed on the top of a low, grassy ridge, about fourteen inches high, formed from material thrown up when a ditch was dug across the marsh, many years before. During some storm a mat of dead 'eel-grass' had been left on top of this ridge, and this had later been lifted by the growing marsh grass, leaving several inches between it and the ground. The nest was placed on the northwest edge of this mat, about half of the nest being under it, while the other side was sheltered and concealed by grass about six inches high. The nest was not sunk in the ground at all."

Two of the nests found were entered from the north-northeast, the other three from the east-southeast. All five nests were sheltered above by stems of black grass. Three of the nests were beneath a layer of dead black grass where a clump of erect living stems parted the mat. One nest (pl. 4, fig. a) was situated where cattail stubs held the black grass somewhat erect. Green stalks as well as dead stalks were woven into a canopy over this nest. Another nest was constructed on a mat of black grass under and among numerous horizontal living stems, some of which were woven into the outer lining of the nest (pl. 4, fig. b).

Nests of both species were found in tussocks of black grass. The locations of these sites differed. The Sharp-tailed Sparrow prefers the higher and therefore dryer portions of the marsh where black grass is the characteristic plant. Contrastingly the Seaside Sparrow almost always chooses the wetter portions of the marsh (Cruickshank, 1942:45; Forbush and May, 1939:514; Stone, 1937:906; personal observations) where several species of plants are abundant. In areas that have been ditched, as have almost all marshes in New Jersey, the mound of excavated muck is ideal for the growth of marsh-elder. Rows of these bushes are present on many of the marshes of New Jersey (pl. 3, fig. a). The location of four of the eight Seaside Sparrow nests in these "hedgerows" indicates that they provide suitable, if not preferred, sites for the species.

EGGS AND INCUBATION

I found no nests of either species before they contained a complete complement of eggs and therefore was unable to ascertain the incubation period for these species. Brood patches were evident on female Sharp-tailed Sparrows by June 1, probably indicating that laying began near this date. Cruickshank (1942:456) lists egg dates of the Sharp-tailed Sparrow as concentrated in early June, with extremes of May 19 and August 4. He thinks the species probably has two broods. For the Seaside Sparrow, Cruickshank (1942:458) states there is probably but one brood and that egg dates are concentrated in early June, with extremes May 23 and July 2. Stone (1937:907, 911) considers four eggs a normal clutch for both species, but cites instances where three and five eggs were thought to be complete sets. Four of the eight Seaside Sparrow nests I found contained at least three eggs, and four contained at least four eggs. Four of the five Sharp-tailed Sparrow nests I found contained at least three eggs and one contained four eggs.

Female Seaside Sparrows do all of the incubation. The male, while the female is on the nest, remains a short distance away. He sings often and gives alarm notes when there is a local disturbance. These chipping notes bring the female off the nest, and then they both chip at the intruder. The male accompanies the female to the feeding grounds and normally they return together.

As previously mentioned, male Sharp-tailed Sparrows take no part in the nesting activities.

YOUNG

I studied growth and changes in behavior of the young. Since I could see no behavioral differences between the nestlings of the two species, this subject will be discussed jointly for the two forms.

Growth

The color of the natal downs of both species is similar. Dwight (1900:190), who saw newly hatched nestlings only of the Sharp-tailed Sparrow, described the color as grayish wood-brown. A series of white neossoptiles is present at the posterior end of the ventral tract in both species. These feathers are more numerous in the Seaside Sparrow. Dwight (1900:98) saw no neossoptiles on the underparts of any of the passerines he examined. Seaside Sparrows have a mid-dorsal row of downs in the dorsal tract near the uropygium. These feathers are lacking in the Sharp-tailed

Sparrow and constitute the major difference, in this plumage, between the two species. The neossoptiles of three Seaside Sparrows and one Sharp-tailed Sparrow were counted. These counts were checked on the young birds studied in the field. The number and placement of these feathers appear in plate five. There appears to be a consistently greater number of natal downs in Seaside Sparrows, when compared with Sharp-tailed Sparrows.

Seven nestling Seaside Sparrows and five nestling Sharp-tailed Sparrows were weighed at 24-hour intervals until they left their nests. The birds were weighed in early morning before they had received much food. Weights of these individuals, and daily averages for each species are shown in Table 1. The weights in the zero column were of nestlings that had not been fed. The weight of one hatchling (1.9 gm.), which does not appear in the table, is included in the average for the zero column. Two young Seaside Sparrows, approximately a week old, fell out of a nest between 9:30 a. m. July 6 and 5:30 a. m. July 7. When I found

TABLE 1—DAILY WEIGHT IN GRAMS OF NESTLING SEASIDE SPARROWS AND SHARP-TAILED SPARROWS FROM LAVALLETTE, OCEAN CO., NEW JERSEY.

Day	*Ammospiza maritima*							Average
0	......	2.2	2.3	......	......	2.2	1.8	2.1
1	3.0	3.3	3.5	3.7	3.3	2.6	2.1	3.1
2	4.6	5.0	5.2	5.0	4.8	3.7	3.0	4.5
3	7.0	5.5	7.2	6.9	6.9	5.9	4.7	6.3
4	9.4	8.1	10.6	9.1	9.1	7.6	6.4	8.6
5	12.5	11.1	12.3	11.4	11.1	9.9	8.7	11.0
6	14.6	13.1	*11.1	13.9	13.7	12.6	9.6	13.0
7	*11.6	13.9	12.1	15.1	14.8	14.3	11.8	13.7
8	14.9	15.5	13.4	14.9	14.8	14.6	12.4	14.4
9	15.2	15.8	13.8	16.2	16.1	16.0	14.4	15.4
10	......	......	......	......	15.9	15.5	14.3	15.2

Day	*Ammospiza caudacuta*					Average
0	1.6	......	1.8	1.7	1.7	1.7
1	1.8	2.3	2.5	3.0	2.1	2.3
2	3.3	2.7	4.1	4.6	3.1	3.6
3	5.0	3.7	5.9	6.4	4.7	5.1
4	6.8	5.4	8.4	9.1	6.7	7.3
5	8.6	6.9	10.7	11.2	9.5	9.4
6	10.2	8.9	12.8	13.0	10.9	11.2
7	12.1	11.4	14.5	13.6	12.3	12.8
8	13.5	12.9	15.3	14.5	13.3	13.9
9	12.2	13.4	15.9	14.9	13.6	14.0
10	12.7	14.0	15.5	15.0	14.0	14.2
11	......	......	......	15.1	14.4	......

* These weights are not figured in the averages; see text.

them below the nest, at the latter time, their temperatures were far below normal, and they had lost a considerable amount of weight. These abnormally low weights were not figured in the averages.

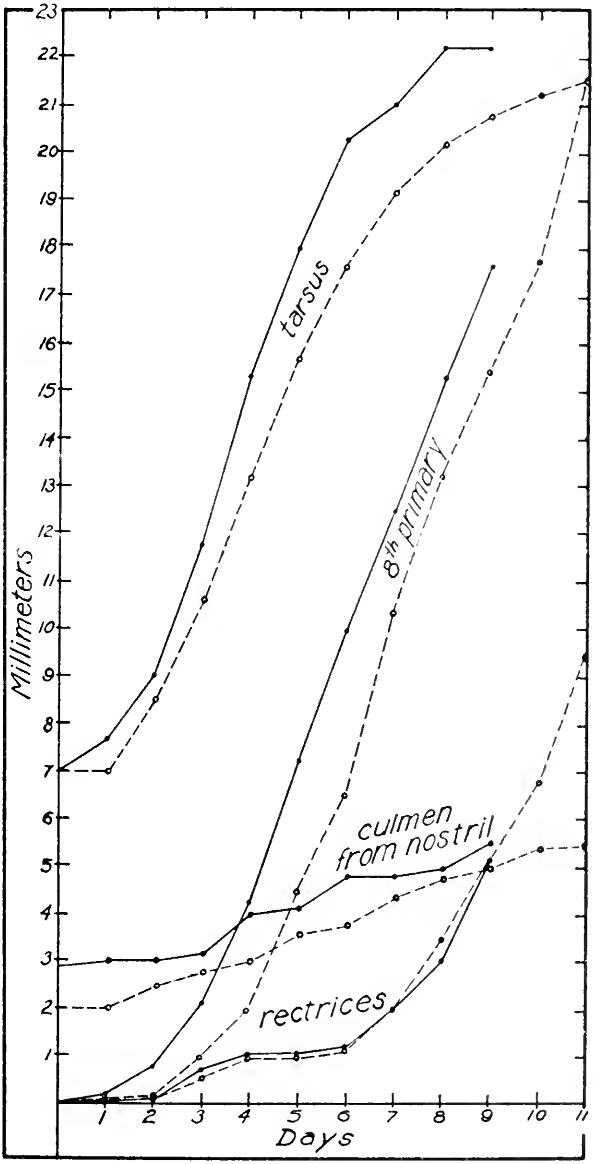


FIG. 1. The development of the young of Seaside Sparrows (solid line) and Sharp-tailed Sparrows (dotted line) as evidenced by four linear measurements taken at 24 hour intervals.

The weights of Sharp-tailed Sparrows 11 days old were obtained by confining the birds to the vicinity of the nest with a screen.

At hatching and throughout nestling life and post nestling life Seaside Sparrows average heavier than Sharp-tailed Sparrows of comparable age (Table 1). Weights of adults of the two species that were netted or collected between May 6 and June 27, 1955, within two miles of Chadwick, Ocean County, New Jersey, follow: Fourteen males of *Ammospiza maritima* averaged 24.2 gm. (21.9-27.4 gm.); three females averaged 22.3 gm. (19.8-24.4 gm.). Thirty-three males of *A. caudacuta* averaged 20.7 gm. (18.0-23.1, 25.8 gm.); 14 females averaged 17.8 gm. (15.3-19.0 gm.), 2.9 gm. less than the males. One female Sharp-tailed Sparrow, weighing 23.1 gm., was not included in the averages because it had an egg with shell in the oviduct.

Montagna (1940:195-196) weighed a series of breeding Sharp-tailed Sparrows (21 males; 5 females) from Popham Beach, Maine, and found the males to be only 0.2 gm. heavier than the females, but he stated that the small number of females weighed, and the high percentage of these that contained eggs, probably lessened the difference in weight found at other seasons.

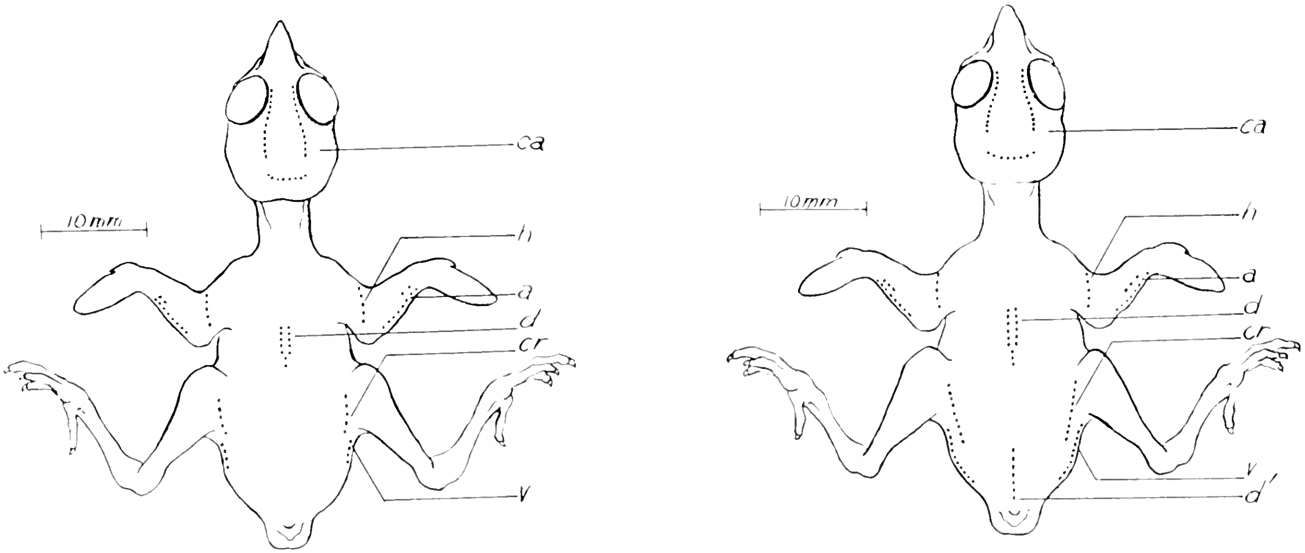
The four linear measurements that I took on the same series of adults confirmed the size difference: Seaside Sparrows average larger than Sharp-tailed Sparrows, and males average larger than females in both species. The average and range for each measurement taken on the sparrows is presented in Table 2.

Four linear measurements were also taken daily on the young sparrows. A summary of these data appears in Figure 1.

Behavior

The first indication of hatching is a crack in the side of the egg along the line of greatest circumference. The crack is extended along this line by the egg tooth, and then contraction of muscles of the neck by the embryo separates the shell into two pieces. Extension of the legs frees the bird from the shell. I held the eggs of two Seaside Sparrows in my hand and watched this procedure. In each instance the young bird defecated in the shell before freeing itself. A barely audible "peep" note was heard from one hatchling Sharp-tailed Sparrow when I held it near my ear. When free from the shell, the young birds rest on their tarsi, abdomen and forehead; their down dries in a few minutes, and their skin becomes noticeably darker. One sparrow gaped five minutes after hatching

PLATE 5



Ammospiza caudacuta

Ammospiza maritima

Drawings of the nestlings of the two species of *Ammospiza* approximately three days of age showing the variation in the amount and placement of the neossoptiles in the two species. Abbreviations for feather tracts in which downs were found: ca, capital; h, humeral; a, alar; d, d′, dorsal; cr, crural; v, ventral.

PLATE 6

An aerial view of the marshes at Chadwick (upper left) and Lavallette (lower left). The Atlantic Ocean appears in the upper right of this photograph.

TABLE 2—LINEAR MEASUREMENTS IN MILLIMETERS OF ADULT SEASIDE SPARROWS AND SHARP-TAILED SPARROWS CAPTURED OR COLLECTED WITHIN TWO MILES OF CHADWICK, OCEAN COUNTY, NEW JERSEY, BETWEEN MAY 6 AND JUNE 27, 1955.

Ammospiza maritima

	14 males	3 females
wing (chord)	64.14 (60–66)	58.33 (58–59)
tail	55.28 (54–59)	51.00 (49–53)
tarsus	23.00 (22–25)	22.17 (21–23)
culmen	15.18 (15–15.5)	14.50 (13.5–15.0)

Ammospiza caudacuta

	33 males	15 females
wing (chord)	58.79 (55–61)	55.67 (54–58)
tail	49.48 (46–53)	46.93 (45–50)
tarsus	20.91 (20–22)	20.30 (20–21)
culmen	13.67 (13–14)	13.23 (12.5–14.0)

and all the young gaped later the same day. The abdomen of the young becomes distended when they are fed by the parents.

In the first 24-hour period after hatching the soft "peep" note is heard frequently. The young are better able to right themselves, and many feather papillae show distinctly through the skin.

On the second day young are capable of moving short distances by using their wings and feet. A thick ridge of tissue forms over the eyeball where the eyelids later delaminate. The call is now a double version of the "peep" note described above.

When the young are three days old the eyelids open, but only slightly. In the next three days the young become better co-ordinated and the eyes open fully. The egg tooth was last seen on a young bird on the sixth day. All incoming feathers remain sheathed until the seventh day.

On the seventh day young show the first signs of cowering. Previously, they all begged when I came to the nest. The remiges remain sheathed, but the body feathers emerge from the tips of the sheaths. A quiet reedy call replaces the "peep" note. A quiet, but squealing distress call was also first noted on the seventh day, when the young were handled.

On the eighth day the remigial sheaths become gray (previously they were dark blue) and begin to slough off. When removed from the nest, the young attempt to escape. Begging is less frequent and cowering is the predominant attitude towards intruders.

The first young of both species left the nest on the ninth day. It must be remembered, however, that this remark, and succeeding remarks, concerning departure of young from nests pertains to young that were disturbed daily by me. The others climbed to the edge of the nest when they were left alone, but remained in the nest when they were all replaced. Gaping was recorded once on the ninth day. Stuart W. John watched two Sharp-tailed Sparrows on my study area leave a nest. They climbed out and immediately hid in a tussock of grass a few inches behind the nest.

On the tenth day when I parted the branches over one Seaside Sparrow nest, the four young jumped from the nest and scattered in the grass. One of these birds gave a chipping note similar to the distress call of adults. No bird remained in a nest longer than ten days. Four young left the nest after nine days, seven young left on the tenth day. When the young leave the nest they are able to run rapidly through the dense grass. The young are fed by the parents for approximately 20 days after they leave the nest. Twenty-three days after one young Seaside Sparrow left the nest it was netted at the opposite end of the island, 300 yards from the territory of its parents.

Young Seaside Sparrows fly in an uncertain but characteristic manner when they are flushed from the grass. They dive clumsily into the grass after a short flight, making it easy to identify them as birds of the year.

The plumage of sparrows of the Genus *Ammospiza* serves to conceal them in their habitat. In juvenal and adult plumage, the Sharp-tailed Sparrow is a brown-backed, streaked bird, the color and pattern blending with the matted grasses (Allen, 1925:67) where the species feeds and nests. The Seaside Sparrow, as an adult, is olive-gray. Its color corresponds to that of the substratum where the species forages. The juvenal plumage of the Seaside Sparrow resembles that of the Sharp-tailed Sparrow. I believe that young Seaside Sparrows have this brown, streaked plumage because they spend most of their time in the dense grass. In the Seaside Sparrow a complete post-juvenal molt begins in late August. The resulting plumage resembles that which is acquired by the adults when they complete their post-nuptial molt (Dwight, 1900:192-193).

FOOD, FEEDING, AND CARE OF THE YOUNG

The food habits of Seaside Sparrows and Sharp-tailed Sparrows have been studied by Judd (1901:64-66), who concluded that both species are highly insectivorous. In 51 stomachs of Sharp-tailed Sparrows 81 per cent of the contents was animal. The results of investigation of stomachs of Seaside Sparrows were similar. In each of the two species the bill is more elongated and less conical than in other sparrows. For the two species studied, the shape of the bill seems to be an adaptation for feeding on insects.

When searching for food, Sharp-tailed Sparrows walk through the dense black grass, deftly brushing stems aside with their bill as they go. Open areas are generally traversed by rapid running. I never noticed either species hopping. They stop to investigate openings in the matted understory of grass, often sticking their heads into the holes. Many times I saw these sparrows stretch or jump to pick insects from stems. Many droppings, almost certainly those of Sharp-tailed Sparrows, were present in areas of damp, matted grass. Females, when feeding young, obtain most of the food near the nest; several times I saw birds catch insects when they were within inches of their nest. Sharp-tailed Sparrows feed also along the banks of pools and creeks, and along the perimeters of marshes. Sharp-tailed Sparrows seem to be less restricted in the types of feeding habitats they can use than are Seaside Sparrows.

Seaside Sparrows always returned to the edge of the marsh to procure food, according to my observations. The birds at Lavallette fed extensively on noctuid moths. In the feeding territories of two pairs of Seaside Sparrows, along the strip of washed-up eel grass, I found at least 40 wings of these moths. In several instances the four wings of one moth were lying close together in the same relative position in which they had been on the animal. Legs and pieces of thorax were also discarded occasionally. I watched adults take these moths from the stems of the smooth cord-grass and snip the wings off with their bills. Moth wings were present in the other feeding territories, but not in so great a quantity. Once I saw a female return to the nest with a spider in her bill. Spiders were abundant throughout the marsh.

Dwight (1900:193) was surprised that the two species living in the same environment, and therefore suffering equally from abrasion from the coarse marsh grasses, should have a different number of molts per year. The Sharp-tailed Sparrow has a complete prenuptial, as well as a complete postnuptial, molt. The Seaside Sparrow has only a postnuptial molt, the nuptial plumage being acquired by wear. My observations of the feeding habits of the two species indicate that they do not live in precisely the same environment. The Sharp-tailed Sparrow, which has two complete molts annually, generally forages in dense, abrasive vegetation. The Seaside Sparrow, which has but one molt each year, forages in relatively open areas.

Several times I saw adult Seaside Sparrows fly from their nests toward the feeding territories with fecal sacs in their bills. On the feeding grounds, I found several of these sacs discarded near the moth wings. I saw also female Sharp-tailed Sparrows leave their nests with fecal sacs. I did not see sparrows of either species swallow fecal sacs.

One nest, that of a Seaside Sparrow containing four young, became fouled with excrement when the young were nine to ten days old. It is interesting that these young were cared for only by a male, at least for the last four days of nest life, and that one of the young birds died two days before the others left the nest. This male's mate was probably a female that I banded on June 18 (the young left the nest on June 23) and never saw again. A female, whose mate was probably killed by me on June 15, continued to incubate the three eggs until they hatched on June 29, but deserted the nest when the young were two days old. This female was seen again on August 1 more than 500 yards from her nest site on the island immediately north of the study area.

Devotion of parent passerine birds to the young typically increases with the growth of the young (Nice, 1943:245). This may explain why the mateless female deserted its nest when the young were only two days old, whereas a mateless male continued to care for his six-day-old young. The death of one nestling, and the eventual fouling of his nest may indicate that the job was too much for one adult to perform. The correlation of increasing devotion of the parents with increasing age of the young was further illustrated by the distraction display, noted by me, on the part of a pair of Seaside Sparrows on the day their young left the nest. As I lifted the four nine-day-old young from the nest for weighing, they began to give the distress call. This attracted the parents from the feeding area approximately 60 yards away. The two adults ran around on the ground within ten feet of me giving the *tsip* note and fluttering their wings. Several times the adults flew within a few feet of me, making a vibrating sound with their wings. Although I realized the function of this display, it was distracting nevertheless.

ACKNOWLEDGMENTS

I am indebted to Assistant Professor Harrison B. Tordoff for comments and suggestions throughout the preparation of this manuscript, and to Mr. Stuart W. John who photographed the birds and the habitat scenes. The aerial photograph of the study island is reproduced with the permission of Fairchild Aerial Surveys, Inc., and the photograph of Lavallette and Chadwick through the kindness of the Lavallette Yacht Club. The drawings were made by Mr. John R. Beeder. Additionally I wish to express my gratitude to Dr. Dean Amadon, Mr. H. Lyman Sindle, and Mr. Lester B. Woolfenden for help and advice in certain aspects of the field work.

SUMMARY

A comparative study of the breeding behavior of the Seaside Sparrow and Sharp-tailed Sparrow was made in New Jersey in 1955.

Observations of marked individuals indicate that the Seaside Sparrow is monogamous and territorial, whereas the Sharp-tailed Sparrow is promiscuous, and at least the male is non-territorial. The male Seaside Sparrow defends its territory by chasing and singing. The male Sharp-tailed Sparrow confines itself to a breeding home range. This range is not a territory; it is inhabited by several males. Female Sharp-tailed Sparrows may be territorial; this is not certainly known.

The Seaside Sparrow sings louder, more distinctly, more often, and from more exposed perches than does the Sharp-tailed Sparrow. These characteristics seem to be correlated with territorial habits. Other calls are described and their functions are discussed.

The Seaside Sparrow nests in marsh-elder bushes, or in areas of mixed vegetation. The Sharp-tailed Sparrow prefers the inner, drier areas of a marsh, where black grass is dominant. The Seaside Sparrow places its nest farther above the ground than does the Sharp-tailed Sparrow. Both species used only black grass in constructing the nest.

Copulation is described. The incubation period was not determined for either species. Three or four eggs seem to be a normal clutch. Females do all of the incubating.

The young remained in the nests nine to ten days. These nests, of course were disturbed, for I visited them at least daily. The nestlings of the Seaside Sparrow are fed by both parents. Male Sharp-tailed Sparrows seem not to know the location of the nests

and take no part in rearing the young at least up to time of fledging. The natal down of both species is described. Data on growth and behavior of the young are presented.

Seaside Sparrows obtained most of their food from the shoreline of the marsh, in areas of open mud and smooth cord-grass. The plumage of the adult matches, in color, this mud. The Sharp-tailed Sparrow feeds everywhere in the marsh, but mostly in areas of dense and matted black grass. The plumage on the dorsum of this species is brown and streaked resembling the dead grass. Juvenal Seaside Sparrows, which spend most of their time concealed in the dense grass, resemble adult and juvenal Sharp-tailed Sparrows in plumage. Sharp-tailed Sparrows molt completely twice per year. The Seaside Sparrow molts but once per year. The difference in number of molts, too, is correlated with habitat preference, since the grassy forage habitat of the Sharp-tailed Sparrow must result in greater abrasion of the plumage than does the open feeding habitat of the Seaside Sparrow.

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Transmitted June 14, 1956.

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26-4360

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MUSEUM OF NATURAL HISTORY

Volume 10, No. 3, pp. 77-127, 2 pls., 7 figs. in text, 4 tables
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UNIVERSITY OF KANSAS
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PRINTED BY
FERD VOILAND, JR., STATE PRINTER
TOPEKA, KANSAS
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Introduction

In northeastern Kansas, before it was disturbed by the arrival of white settlers in the eighteen fifties, tall grass prairies and deciduous forests were both represented. These two contrasting types of vegetation overlapped widely in an interdigitating pattern which was determined by distribution of moisture, soil types, slope exposure and various biotic factors.

The early explorers who saw this region, and the settlers who came later, left only incomplete descriptions, which were usually vague as to the locality and the species of plants represented. As a result, there is but little concrete information as to the precise boundaries between the forests and grasslands, and opinions differ among ecologists. No representative sample of either type remains.

It may be assumed that the plant communities existing one hundred years ago and earlier were far more stable than those of the present that have resulted from man's disruptive activities. This stability was only relative, however. Within the last few thousand years since the final withdrawal of the Wisconsinan ice sheet, fairly rapid and continual change must have occurred, as a result of changing climate, the sudden extinction of various large, dominant mammals, and finally the impact of successive aboriginal cultures.

The land north of the Kansas River had been a reserve for the Delaware Indians. This land was thrown open to settlement as a result of two separate purchases from the tribe, in 1860 and 1866. The alluvial bottomlands were fertile and soon were under cultivation.

History

Because the prairies and forests were soon destroyed or altered by cow, ax, plow and fire, knowledge of the region's ecology under the conditions that prevailed in the early nineteenth century and the centuries before must be gained largely from circumstantial evidence. Although there were no ecologists among the first settlers in Kansas, occasional glimpses of the region's ecology are afforded by the writings of early residents who mentioned native plant and animal life from time to time. However, such mention was usually casual and fragmentary.

A brief early description of forest in northeastern Kansas, which is casual and incomplete, and perhaps misleading, since it differs from later accounts, was included in Major W. S. Long's report of the exploring expedition that passed through country now included in Johnson, Douglas, Shawnee, Wabaunsee, Riley, Pottawatomie, Jackson, Jefferson and Leavenworth counties in 1819. "The catalogue of the forest trees in this region is not very copious. The cottonwood and the plane tree [sycamore] everywhere form conspicuous features of the forests. With these are intermixed the tall and graceful acacia, the honey locust, and the bonduc, or coffee-tree, and carya [hickory] and fraxinus [ash] . . ." (Taft, 1950:442).

A description of the country in northern Douglas County and adjacent Leavenworth County, while it was still in virtually undisturbed condition, was written by Mr. George S. Parks (1854). Travelling up the Kansas River from the Missouri state line he described the vegetation and physiography with respect to specific landmarks that can be easily located at the present time. His descriptions of the areas he saw that were nearest the Reservation, are quoted below, in part.

[Travelling west from near the mouth of Stranger Creek 10 miles ESE Reservation.] ". . . bluff with open woods and high rolling prairie in background. On the south side of the river . . . grass and scattering timber forming a green lawn back with high prairie. In this neighborhood the shore is rocky. We passed a bald bluff on the north, with a rich bottom on the south side, and a high open lawn in the rear. A little farther on the elevated prairies strike the river, giving a charming variety of scenery—while on the north are extended bottoms of rich timbered lands.

"In this vicinity we saw many Indians along the banks; we also passed a grape thicket, in the bottom, spread over several thousand acres—while just above, on our right, rose a rocky bluff, covered with open woods. A little above this Sugar Creek empties into the Kansas, from the right; and a little farther up, there is a low bluff—a short distance beyond, there being another fine grape thicket, and rich walnut bottom. On the right side of the river . . . rises a beautiful undulating eminence . . . open woods and a fine prairie about a mile back.

"On the left, a short distance above, the Wakarusa flows in—a considerable stream—with good timber for some way back.

"On both sides of the river, above the Wakarusa, there are excellent bottom lands; . . . farther up on the south bank, the high prairie comes down to the water's edge. . . . away as far as the eye could reach in a southwest direction, the prairies were high and rolling, like the waves of old ocean—southward, beautiful groves dot the prairie and the dark line of timber that stretches along the Wakarusa Valley—with the great Prairie-mound . . . fixed there as a landmark of perpetual beauty—the meandering river with its dark skirting forests of timber on the north . . . Proceeding north, high rich bottoms extend for many miles and we saw vast thickets of grape-vines, pea-vines etc. and paw-paws. The timber was principally oak, walnut, ash, hickory, mulberry, hackberry, linden, cottonwood and coffee-bean.

[Between the Reservation and the mouth of the Delaware River, 10 miles west.] "A few miles below the mouth of the Grasshopper [Delaware] on the north the prairie undulates gradually back from the river as far as the eye can reach . . . between the Grasshopper and Mud Creek there is a prairie bottom where pioneers are making claims."

In 1855 Mrs. Sara T. D. Robinson, wife of Dr. Charles Robinson who was the first governor of Kansas, described in her diary the environs of Lawrence (1899). In part, the areas described by her overlap those described by Parks, and both writers impart similar impressions. Mrs. Robinson's writing was concerned chiefly with the social and political affairs of the territory and the occasional comments on the "scenery" in her voluble accounts must be regarded as impressions rather than purposeful and accurate descriptions, as certain inconsistencies are apparent. Excerpts from several of her more significant descriptive passages are quoted below. [Between Lawrence and Kansas City, April 17, 1855.] ". . . prairie stretching in all directions, noble forests marking the line of the rivers and creeks, . . . tall oaks and walnuts grouped in admirable arrangement . . . there were deep ravines . . . skirted with graceful trees, while the water in their pebbly beds is limpid and clear." [North of Wakarusa Crossing.] ". . . stumps in every direction in the woods . . ." [At Lawrence, April 18, 1855.] "The town reaches to the river, whose further shore is skirted with a line of beautiful timber, while beyond all rise the Delaware lands, which in the distance have all the appearance of cultivated fields and orchards . . . A line of timber between us and Blue Mound marks the course of the Wakarusa, while beyond the eye rests upon a country diversified in surface, sloping hills, finely rolling prairies, and timbered creeks. . . . to the northwest there is the most delightful mingling together of hill, valley, prairie, woodland, and river. . . . fine grove about a mile west of town, one of Nature's grand old forests."

[On trip to visit a neighbor four miles away from Lawrence.] "There were high, conical hills, bearing on their tops forest trees, with dense, thick foliage; at the next moment a little shady nook, with a silvery rivulet running over its pebbly bed . . ."

[On trip west toward Topeka.] "Timber was more abundant, not only marking the line of the creeks, but crowning the summit of many an elevation."

[At Lawrence.] "Lawrence and its surroundings, of river flowing beneath the dim forests two miles deep on the north bank . . ."

Parks' and Robinson's accounts seem to show that in general bottomlands and stream courses were wooded, and uplands were mainly prairie, but that local deviations from this pattern were numerous, with trees and groves isolated or partly isolated in a variety of situations. This condition suggests that prairies were then encroaching into formerly wooded areas. A climatic shift toward hotter and drier conditions, or a change in native practices, with more frequent burning, might have brought about the trend.

Further information concerning the distribution and composition of the forest is afforded by a series of letters from the settlers at Lawrence, Kansas, that were printed in various Boston newspapers and in the Milwaukee Daily Sentinel, in 1854, 1855, and 1856. In nine such letters which discuss, among other things, the availability of timber, several kinds of trees are listed. Oak (species not mentioned), black walnut, and cottonwood are each listed in seven of the nine letters, while elm, hickory and "white walnut" are each listed in two, and ash, hackberry, sycamore, basswood, willow and locust are each mentioned only once. Copies of these letters are in the files of Dr. James C. Malin, to whom we are much indebted for the privilege of examining them, and for his critical reading of parts of the manuscript.

Early U. S. Government maps of northeastern Kansas show the distribution of forest in the late eighteen fifties, and in general the pattern agrees well with that indicated by the accounts of Parks and Robinson. Through the kindness of Dr. Malin, we have been permitted to examine his photostatic copies of a series of these early maps, covering the area discussed in our study, and made in the period extending from 1855 through 1860. A tracing taken from parts of two of these maps, showing the Kansas River north and east of Lawrence, and the area between the river and the north boundary of Douglas County, is reproduced in Fig. 1. For comparison, a map of the same area showing the stream courses and the distribution of timber, as traced from recent U. S. Geological Survey maps, is reproduced in Fig. 2.

The early maps agree with Parks' and Robinson's descriptions in showing an extensive belt of timber in the flood plain north of the river, and narrower belts of timber along its tributary streams. In Fig. 1 the courses of the Kansas River and of Mud Creek agree fairly well with those shown on modern maps, but there are gross errors in the minor drainage systems of the sections of land in the northeastern part. Other evidence indicates that the distribution of forest was much different than that shown in this part of the map. Field work by the map-makers in this marginal area must have been extremely sketchy. Dr. Malin explains that such inaccuracies are to be expected because the contracts for mapping were made on a political basis, with little or no regard for other qualifications of the applicant.

The University of Kansas Natural History Reservation is in the northeasternmost section (Section 4, Township 12S, Range 20E) of Douglas County, Kansas. Topographically, it is almost evenly divided into three parts: (1) peninsular extensions of the Kansas River Valley, sloping gradually up to a level approximately 100 feet above that of the flood plain; (2) hilltops 200 feet or more above the level of the flood plain; (3) steep slopes from the hilltops to the valley floor.

The land that is now the Reservation was part of a tract acquired in the eighteen sixties by former governor Charles Robinson, after the Delaware Reserve lands in the northeastern part of Kansas Territory were sold by the tribe. The section of land now comprising the Reservation was used primarily for grazing after Robinson acquired it. However, several squatters settled on the area and cultivated small acreages for periods of years in the eighteen seventies and eighteen eighties. In the eighteen nineties parts of the area including some of the hillsides were still covered with a mixed forest of virgin timber (*fide* Frank H. Leonhard in conversation, October 19, 1951). Mr. Leonhard, who was long in the employ of the Charles Robinson family, remembered the area as far back as the early eighteen nineties when he worked on it cutting timber. He remembered, especially, cutting large walnut trees as much as two

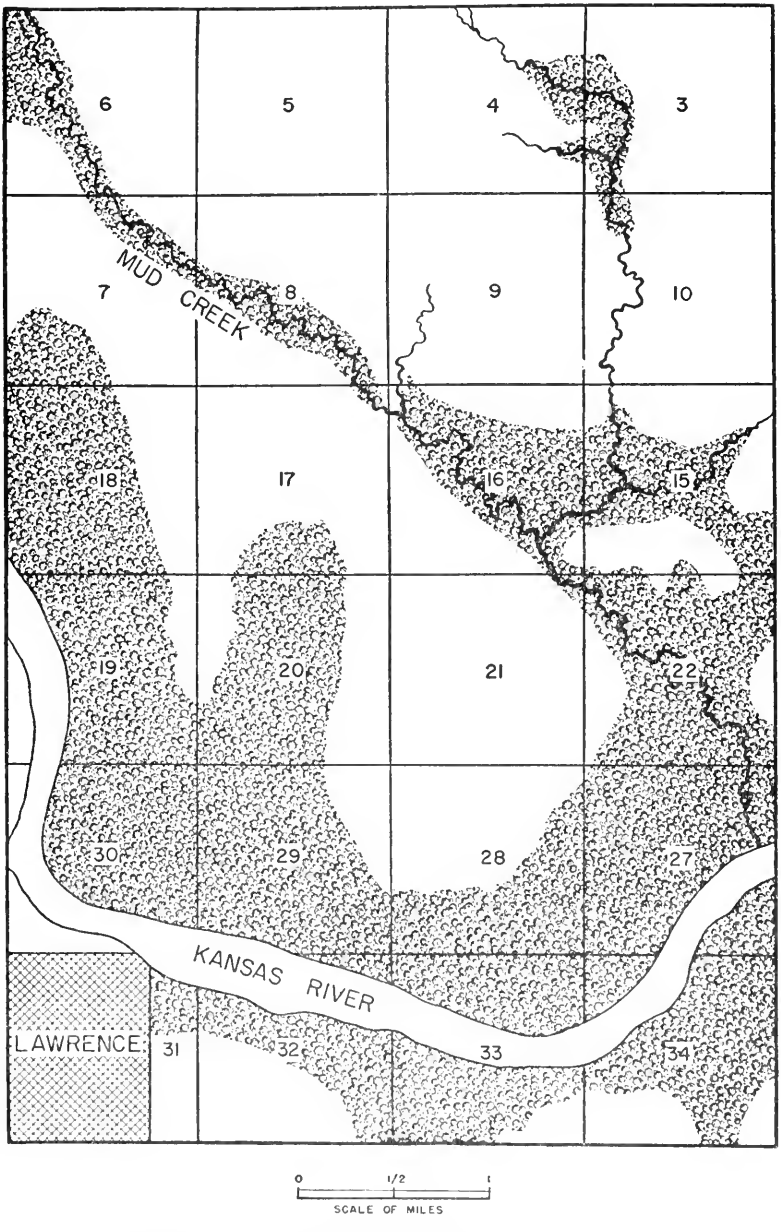

FIG. 1. Tracing from early (1855-60) U. S. Government maps of northeastern Douglas County, Kansas, and adjacent western edge of Leavenworth County, showing stream courses and approximate distribution of woodland before deforestation had occurred. Section 4 to right of center at upper edge of figure, is now mostly included in the University of Kansas Natural History Reservation. Note inaccuracies in drainage systems on this part of map as compared with Fig. 2.

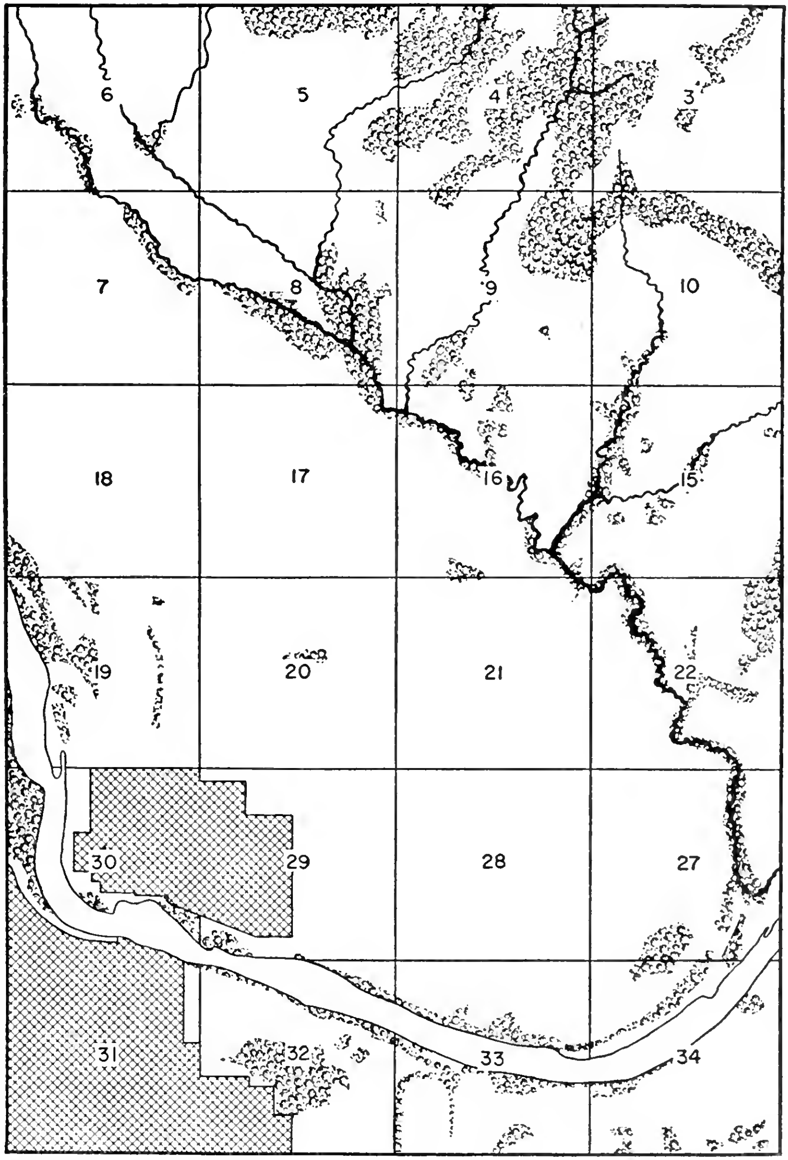

FIG. 2. Tracing from 1950 U. S. Geological Survey maps of same area shown in Fig. 1, indicating present distribution of woodland, and the pattern of drainage systems.

feet in diameter, which were valuable timber, but he thought that elm also was abundant at that time. By then the area, separated into east and west halves by a rock wall, had already been heavily grazed, and the original prairie vegetation, presumably dominated by big bluestem, had been much altered. The open upland portions were dominated by blue grass.

By about 1900 control of the area had passed to the J. F. Morgan family. The homesteads had long since been deserted and the entire area was used for grazing (*fide* J. F. Morgan, in conversation, January 13, 1952). Parts of the bottomland were fenced and broken for cultivation in 1907, 1912, and 1915, and hilltop fields were first cultivated in 1909. Tree cutting was more or less continual. Many of the old stumps still present on the area are remnants of the trees cut in the "twenties" or even earlier. Several acres of hilltop and south slope in the northwest corner of the area were protected from livestock and maintained for harvesting of prairie hay. The hay was mowed annually, and the vegetation was burned at less frequent intervals, usually in early spring. This treatment served to kill encroaching woody vegetation and to maintain a prairie type.

In the mid-thirties control of the area passed to the University of Kansas. At that time a program of development was launched by the University and the U. S. Soil Conservation Service with relief labor (*fide* C. G. Bayles in conversation, November 10, 1953). The work included: filling gullies, digging diversion ditches and building check dams and terraces to prevent erosion; clearing extensive thickets; bindweed eradication from the cultivated areas; and fencing off the wooded hillsides from the valley and hilltop pastures for protection from livestock. This work extended over several years, and one main objective was to utilize the area for growing timber. However, plans to make extensive plantings of walnut and other valuable timber never materialized. In the forties the check dams fell into disrepair. The area was leased to a farmer and was again heavily overgrazed. In this period there was some tree-cutting by the University's Department of Buildings and Grounds and by farmers, but this cutting was not on a commercial scale and was mainly for firewood and fence posts. One of the chief results of fencing off the wooded hillsides was that shrubs and young trees, formerly held in check by livestock, were allowed to flourish. Understory thickets sprang up throughout most of the woodland, and especially in edge situations.

Late in 1948, after the area had been made a Reservation, livestock were excluded. In the years following, the parts of the closely grazed pastures adjacent to woodland passed through stages similar to those that had occurred 10 to 12 years earlier in the parts protected by fences. Young trees and shrubs sprang up in thickets, the numbers and kinds depending on amount of shade, seed sources, soil, moisture, and various other factors.

Although most of the tree-cutting was done prior to 1934, annual growth rings are discernible on many of the old stumps, indicating the age of the tree at the time it was cut. Occasionally the stumps produced sprouts which had grown into sizable trees by 1954. In such instances the year that the tree was cut and the year that it originally began growing could be determined from a study of the annual growth rings. In 54 instances ring counts were obtained from stumps or logs, or from trees that had been split and fallen in wind storms.

Stumps that were otherwise intact often had small central cavities an inch or more in diameter. For these it was necessary to estimate the numbers of missing rings in order to obtain a figure for the approximate total age of the tree at the time it was cut. Many of the logs and stumps were so much decayed that growth rings were no longer distinct, and on most there were a few rings that were not clearly defined. In the majority of instances the time of cutting could not be determined accurately, but it is known that there was little tree-cutting after 1934 on most parts of the area. Probably most of the stumps on the Reservation that were well enough preserved to provide counts were from 20 to 30 years old. Most of the counts of growth rings on chestnut oaks were obtained on a hillside adjoining the Reservation where the trees were cut in the early nineteen forties.

Width of the annual growth rings reflects rapidity of growth in the tree and is determined, in part, by the amount of annual rainfall, especially in this region on the western edge of the deciduous forests where moisture is the chief limiting factor. Periods of drought or of unusually heavy rainfall may result in growth rings smaller or larger than average. Because the trees draw moisture from the deeper soil layers, there is a lag in their response to precipitation, and a single year that is much wetter or much drier than those preceding or following it may not stand out clearly in the annual rings. In individual trees the effect of precipitation is often obscured by the effects of crowding and shading by competitors, injury or disease. None of the trees examined for growth rings reflected the annual precipitation accurately for long periods though some indication of known drought periods or of series of wet years were usually discernible.

For 35 black oaks, chestnut oaks, and American elms, growth rings averaged 3.81 per inch of trunk diameter (according to size of the tree; 5.1 rings per inch in those trees 9 to 12 inches in diameter, 4.0 in those 13 to 15 inches, 3.6 in those 16 to 24 inches, and 2.8 in those of more than 24 inches). Data from a few complete counts and many incomplete counts indicate that in *Gleditsia triacanthos* growth is much more rapid, with only 2 to 3 rings per inch of trunk diameter, whereas in *Juglans nigra, Celtis occidentalis, Carya ovata,* and *Fraxinus americana* growth is much slower, with usually five or more growth rings per inch of trunk diameter. Individual trees deviate widely from the average for their species, and those in rich bottomland soil grow more rapidly than those in shallow soil of hilltops or those on rocky slopes. If such factors are taken into account the ages of trees may be estimated from the diameters of their trunks. In mature trees growth slows; age is likely to be underestimated rather than overestimated in those of exceptionally large size.

The belief that this and similar areas in northeastern Kansas were virtually treeless at the time of occupation by white settlers is shown to be wholly unfounded by the information obtained from growth rings. The ring counts show that many trees now growing on the area and others cut within the last 30 years, but still represented by stumps, were already present in the eighteen sixties when the area was first occupied. A few trees on the area probably are much older, dating back to the early eighteen hundreds. As there are no virgin stands of timber, and the more valuable trees have been removed by selective cutting at various times, it is to be expected that there are few or no trees on the area approaching the potential longevity for their species.

The many oaks and elms on the area that are more than two feet in trunk diameter mostly date back to the eighteen sixties or earlier. The distribution of the larger trees and stumps provides a clue as to the original distribution of forest and grassland on the area. There is no description available of the area that is now the Reservation in its original condition. However, Mrs. Anna Morgan Ward (1945) has recorded comments on the appearance of the country in the section of land adjoining the Reservation on the south, as it appeared when her family settled there in 1864. This land differed from that of the Reservation, as it consists of low rolling hills, well drained with predominately south exposure, and with sandy soil. It adjoins the present flood plain of the Kansas River, and consists partly of the old Menoken Terrace deposited in the Pleistocene. The following excerpts from Mrs. Ward's manuscript are selected as most descriptive of the original vegetation on this section of land.

[In southwest part of section near the Morgan house.] ". . . some hills that were covered with Jack Oak trees . . . Here we found wild strawberries on the hillsides. And along the creeks we located gooseberry bushes, wild grapes, both summer and winter grapes, plums, and paw paws in the fall. We found a crabapple tree . . . Plenty of walnuts and hazel nuts."

[Hilly south-central part of section, the J. P. Whitney farm.] ". . . on a hill among many small trees . . . especially on the east were many trees."

[Less hilly southeastern part of section.] ". . . Was open prairie and free grazing ground for many years. . . ."

Much of the land in this section is now under cultivation but there are still hilltop groves of blackjack oak, probably in about the same places where Mrs Ward noticed them 90 years ago—south of the house that was formerly Robinson's residence, and west across the county road, beside the Oakridge School building, and on other knolls to the east and southeast.

The bottomland areas of the Reservation are mainly grassland and no old stumps remain to indicate that trees were formerly present. Nevertheless, it might be expected that under original conditions these bottomland areas supported forests, as the soil is deep and rich with abundant moisture. Also most of the early accounts agree that forests occurred mainly along stream courses in this region. Presumably these areas were cut over early, because they were most accessible, and because they supported the best stands of timber.

One of the best indications of the former vegetation on these bottomland areas is provided by old bleached shells of snails and certain other mollusks, brought to the surface by plowing in cultivated fields adjoining the Reservation on the south and west (Fitch and Lokke, 1956). A high proportion of the shells are of species limited to humus soil, decaying logs, or leaf litter in moist woodlands (*Stenotrema leai, Retinella electrina, Zonitoides arboreus, Vertigo ovata, Helicodiscus parallelus*), to wet places (*Lymnaea parva, Suc-*

cinea avara) or even to standing pools (*Physa hawni, Helisoma trivolvis, Pisidium compressum*). No living mollusks could be found in these fields and none could be expected to survive on land that is cultivated annually. As a whole the assemblage seems to be indicative of a humid, poorly drained forest habitat. Presumably most of the shells or all of them are more than 100 years old, antedating the time when the area was first disturbed by human activities, and also antedating the time when the creeks (now 15 feet or more below the fields) had begun to erode their channels. That the shell deposits are of no great antiquity, and represent conditions prevailing within the last few hundred years, is suggested by the fact that all are species still living in Douglas County, and with one exception, all still live on the Reservation.

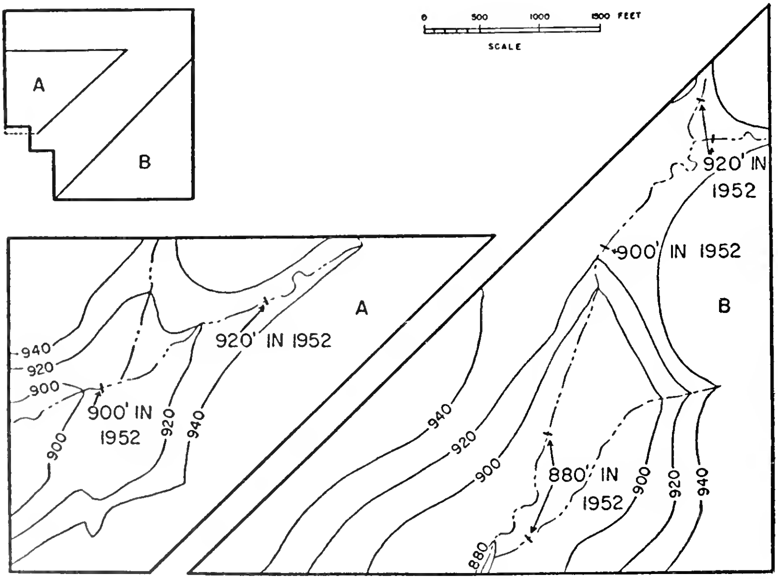

Fig. 3. Tracing from a contour map made in 1914, of the two small valleys on the Reservation, showing changed position of contour lines at gullies by 1952. As a result of overgrazing, and cultivation of part of the upland drainage area, there was relatively rapid erosion in the 38-year interval.

Mrs. Ward (*op. cit.*) in her manuscript concerning the early history of Grant Township, mentioned the small creek that drains the east part of the Reservation. Evidently in the sixties it had a more constant flow, usually with clear water. Later it eroded its channel, cutting a deep gully. Presumably the water table has been much lowered. In his verbal reminiscences of the area, Mr. J. F. Morgan told us that in the nineties this stream had eroded its channel but little within the present limits of the Reservation. In a period of years, 1902 to 1905 inclusive, when there was abnormally heavy rainfall, severe erosion occurred, and the saturated soil of several hillside areas slipped downhill to the extent of several feet vertical displacement. The ravine draining into the present pond from the north was known as "Sunken Canyon" because of such soil slips. However, a map of the Reservation and surrounding areas made by the University of Kansas Department of Civil Engineering in 1914, shows that by that time relatively little gullying had occurred. Com-

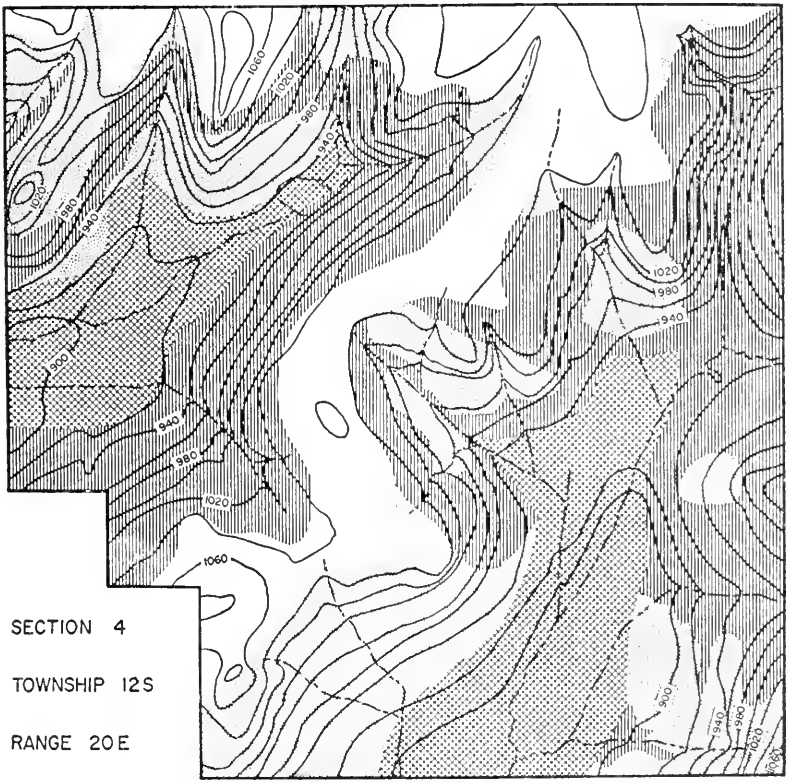

Fig. 4. Map of University of Kansas Natural History Reservation, with 20-foot contours, showing probable approximate distribution of forest in early eighteen hundreds (vertical lines show slopes and hilltops that are still wooded; grid pattern shows bottomlands that were formerly wooded but later cleared for pasture or cultivated crops). Stippled areas show those slopes and hilltops now wooded seemingly as a result of recent reinvasion, that probably were bluestem prairie earlier. Unshaded areas are relatively flat hilltops that are still grassland and are thought to have been bluestem prairie.

parison of this contour map with a more detailed one prepared in 1952 shows that the gullies had eroded their channels to depths more than 15 feet greater in some places, in the 38-year interval (Fig. 3). In June and July, 1951, when there was unusually heavy rainfall, gullies deepened perceptibly. Dozens of trees including many large mature elms, honey locusts, and osage orange, growing along the banks were undermined and fell into the gullies.

Composition of the Forest

Under present conditions, every one of the larger tree species dominates at least some small part of the area. For reasons that are usually obscure, locations that seem otherwise similar differ in the kinds, numbers, and sizes of trees they support. Probably most of these differences have arisen in the varying treatments under human occupation in the last 100 years.

In the two valley areas, presumably heavily wooded under primitive conditions, the trees growing at present seem to be secondary invaders. They include groves and isolated trees of elm, honey locust, walnut, and osage orange, and an occasional red haw, hackberry, or coffee-tree.

The hilltops likewise are chiefly open, but forest of the hillsides encroaches onto them for as much as 100 yards in some plaes. The slopes between the hilltops and the valleys are almost everywhere wooded, but the aspect of the woods changes from place to place. Subdivisions on a vertical scale, might be recognized as follows: the upper limestone outcrop (Plattsmouth member) at the hilltop; the usually steep slope strewn with rocks, between the upper and lower (Toronto) limestone outcrop; the lower limestone outcrop; an almost level terracelike formation often approximately 50 feet wide a few feet below the level of the Toronto limestone; the slope below the terrace, variable in steepness, exposure, and soil type, and usually several times more extensive than the first four subdivisions combined. Along both the upper and lower outcrops, elm and hackberry are especially prominent. Chestnut oak is abundant along the outcrops and on the rocky slope between them in some situations. Ash grows abundantly on some upper slopes but there are few growing on the upper outcrop. On the terrace, elm, ash, hackberry, honey locust, coffee-tree and black oak are abundant. On the lower slopes grow most of the blackjack oaks, post oaks, red oaks and mulberries.

Even greater differences in the local aspect of woodland on the hillsides are caused by slope exposure. On south facing slopes, especially, the woodland is noticeably different from that in other situations, and of more xeric aspect. The climax species, *Quercus Muehlenbergii*, *Q. rubra*, *Q. velutina* and *Carya ovata* are almost totally absent. Such trees as are present are of small to medium size. They are mostly red elm, American elm, walnut, honey locust, hackberry, and osage orange, with dogwood (*Cornus Drummondii*) and plum (*Prunus americanus*) forming dense thickets. Occasional patches of prairie grasses remain in more exposed situations where they have not been shaded out. These, together with the small size of most of the trees, indicate that the south slopes have become wooded rather recently, and originally were prairie. Nevertheless, the small remaining groves of blackjack oak and post oak are on slopes that face south, southeast, or southwest, and probably under original conditions they occupied these situations, separate from the forests of other hardwoods. Slopes facing east, west, and north, are more similar in relative abundance of various kinds of trees, and they do not differ much from hilltop edges that are wooded. Chestnut oak and hickory are most abundant on north slopes, and ash occurs mainly on north slopes.

TABLE 1.—PERCENTAGES OF LARGER TREES (A FOOT OR MORE IN TRUNK DIAMETER) ON DIFFERENT SLOPE EXPOSURES.

	North slopes	Hilltops	West slopes	South slopes
Elm	35.7	38.6	25.8	51.4
Chestnut oak	22.0	18.3	17.8	2.9
Hickory	8.8	4.0	3.6	5.0
Walnut	8.8	5.8	19.6	12.1
Ash	7.1	.8	....	.4
Hackberry	8.2	1.6	2.4	6.9
Black oak	3.3	16.4	....	1.0
Red oak	2.2	....	23.8	....
Locust	1.8	7.5	1.9	11.6
Osage orange	.5	1.5	.2	5.3
Sycamore	.5	....	2.1	.1
Coffee-tree	....	1.2	2.4	1.0
Cherry	....	2.4	....	.1
Red haw	....	.4	....	1.3
Ailanthus	....	....	....	.3
Mulberry	....	.5	....	.1
Cottonwood	....	....	....	.1
Redbud	....	.8	.2	.1
Boxelder	....	.1	....	.3
Blackjack oak	....	....	.2	....
Total trees in sample	182	890	467	898

Table 1 shows the percentages of different kinds of trees a foot or more in trunk diameter on different slope exposures sampled. Elm is almost always the dominant tree, making up from one-fourth to one-half of the total stand. The other species dominate relatively small areas. Chestnut oak usually makes up a substantial part of the stand on hilltops and slopes of north, east, or west exposure. Black oak, red oak, and walnut may be prominent on the east and west slopes. Walnut and locust are prominent on south slopes.

Hickory usually has a trunk diameter of less than one foot, and, therefore, it is not prominent anywhere among the larger trees. Table 2, showing ratios of medium-small trees (more than 6 inches and less than one foot in trunk diameter) demonstrates that hickory is one of the more prominent trees on hilltops and on slopes other than those of south exposure.

Invasion of Fields

In 1948 when the extensive open parts of the Reservation were grazed and cultivated, small trees were inconspicuous and few. Mature trees, with trunk diameters of 9 inches to more than two feet, were distributed over the pastured areas, however, with groves of American elm, honey locust, and walnut near the edges of the woods, and occasional scattered trees of these species and of osage orange, coffee-tree, red haw, hackberry, and ash.

TABLE 2.—PERCENTAGES OF DIFFERENT KINDS OF SMALL TREES (SIX INCHES TO A FOOT IN TRUNK DIAMETER) ON DIFFERENT SLOPE EXPOSURES.

	North slopes	Hilltops	East slopes	South slopes
Elm	29.6	29.9	34.6	57.9
Chestnut oak	29.6	17.5	15.5	.4
Hickory	11.1	25.4	28.4	.8
Walnut	5.6	.7	7.4	5.3
Hackberry	13.0	1.0	3.7	26.4
Black oak	1.9	16.3	....	....
Red oak	1.9	....	6.8	....
Locust	....	3.3	....	3.0
Osage orange	....	2.0	....	1.5
Coffee-tree	1.9	.7	....	1.1
Cherry	....	....	....	.4
Red haw	....	2.4	....	....
Mulberry	....	.7	....	....
Redbud	9.3	....	3.7	.8
Boxelder	....	....	....	2.6
Total trees in sample	54	295	162	266

In 1949 soon after the discontinuance of grazing and cultivation, a large crop of tree seedlings became established. Each year thereafter the numbers were augmented by new crops of seedlings, but conditions rapidly became less favorable for their establishment, as the ground cover of herbaceous vegetation became thicker. The numbers and kinds of young trees that became established differed markedly in different situations. The seedlings present in large numbers were those of elm, honey locust, boxelder, dogwood, walnut, osage orange and crab-apple. There was none of the climax species —oaks or hickories—in the sample.

TABLE 3.—NUMBERS OF YOUNG TREES PER ACRE IN FIELDS OF THE RESERVATION, JUNE, 1952.

	Bottom-land pasture	Hilltop pasture	Bottom-land fallow field	Hilltop fallow field	Prairie
No. of 1/100 acre plots sampled	250	80	70	80	50
Honey locust	83.0	58.8	....	5.6	....
Elm	80.0	72.5	138.8	230.0	150.0
Boxelder	1.6	1.2	22.9	....	200.0
Dogwood	18.8	18.8	11.4	51.2	44.0
Walnut	2.0	50.0	7.15	....	....
Osage orange	16.0	48.7	....	....	....
Crab-apple	7.2	93.8	....	1.2	....
Red haw	5.2	17.5	2.8	2.5	4.0
Coffee-tree	4.8	1.2	....	....	....
Hackberry	2.8	....	....	....	2.0
Cottonwood	.2	....	....	....	....
Ash	....	8.8	....	3.7	....
Plum	.8	....	....	....	....
Peach	.2	....	....	....	....
Cockspur thorn	.8	21.3	....	....	....
Sycamore	.4	....	....	1.2	....
Cherry	....	1.2	....	....	2.0
Total number counted	236	393	279	296	402

Table 3 shows the numbers of young trees counted in a total of 530 plots of 1/100 acre each, in June, 1952. The trees counted included all those approximately one foot high or larger. A few were up to 12 feet tall, but most were between one foot and five feet in height. Not included were the many smaller seedlings, which were mostly concealed beneath the dense layer of low herbaceous vegetation.

Of young trees there were most on the bluestem prairie area, less on the former pastures and least on the fallow fields. In both the pasture areas and the fallow fields, the bottomlands had fewer trees than the hilltops—60 per cent and 94.3 per cent, respectively. In every instance the abundance of young trees seemed to be inversely proportional to the amount of competing herbaceous vegetation. The bottomland fallow fields, which had the fewest tree seedlings, were dominated by a rank growth of giant ragweed and sunflower, often as much as ten feet tall, effectively shutting most of the light from the tree seedlings. By 1954, however, the sunflower was nearly eliminated, and the giant ragweed, though still abundant, was much stunted.

The bluestem prairie on an area of hilltop and upper slope had not been burned over or otherwise disturbed for some years prior to 1948, and probably trees began to invade this area years before they invaded the fallow fields and pastures accounting, in part, for their greater abundance in 1952. Approximately half of the young trees on this prairie area were boxelders, which were relatively scarce on the other four areas. Elm was either first or second in abundance on each area. On both types of pasture areas honey locusts were appearing in abundance and osage orange seedlings were present in somewhat smaller numbers. However, these two kinds of trees were almost entirely absent from the other areas sampled, except that a few locusts were recorded on a hilltop fallow field. In 1948 honey locust seeds were noticed in great abundance in the droppings of cattle; their dispersal in this manner probably is in large part responsible for the abundance of young honey locusts throughout the former pastures. Osage orange may have been distributed in the same manner. Seedlings of dogwood were moderately numerous on each one of the areas sampled, and those of red haw were somewhat less abundant on each area. Crab-apple was the most abundant species invading the hilltop pastures but was scarce or absent in the other situations. The remaining species of trees, including coffee-tree, hackberry, cottonwood, ash, plum, peach, cherry, cockspur thorn, sycamore, and redbud, each made up only a small percentage of the tree crop in the situations where they occurred.

In late July and early August, 1954, counts of young trees were made again on the upland pasture area, with a total of 200 1/100-acre plot samples. This sample was taken at the end of one of the longest and most severe droughts in the history of the area. Both 1952 and 1953 had drought summers, and up to the end of July the summer of 1954 was exceptionally dry also. The conditions of the young trees at this time, in the relatively dry and shallow hilltop soil, was especially significant. As might have been anticipated, in this 1954 count, young trees were more numerous than they had been on any of the areas sampled in 1952. However, the data for 1952 and 1954 are not entirely comparable, because in 1952 none of the plots sampled was nearer than 50 feet to the edge of the woods, whereas in 1954, the sample was arranged to be representative of the entire field, including the parts adjacent to the woods. The numbers per acre of each kind of tree, and the percentages that were dead or dying, were as follows: crab-apple 167 (33.5 per cent dead); locust 98 (3 per cent dead); elm 69.5 (2.9 per cent dead); osage orange 63.5 (none dead); walnut 36.5 (4.1 per cent dead); red haw 25.5 (none dead); ash 19.5 (none dead); cockspur thorn 17 (17.6 per cent dead); wild plum 14 (3.6 per cent dead); dogwood 9.5 (none dead); prickly ash 2 (25 per cent dead); black oak 1.5 (none dead); boxelder .5 (none dead). Thus, of the species that were prominent invaders of the field, only crab-apple showed heavy mortality. In many instances the mortality in crab-apple was due wholly or in part to attack by cottontails (*Sylvilagus floridanus*), which had completely girdled many of the stems. In general, mortality in the young trees was light in this grassland area compared with the mortality in any part of the woodland.

Competition and Mortality

The ratios of trees of different species and different size groups reflect, to some extent, the changes to which the area has been subjected. Under original conditions mature trees of oak and hickory dominated the forest. With the opening up of the forest that resulted from cutting most of these mature trees, other kinds of trees increased and spread. Species relatively intolerant of shading became established. Chinquapin oak, honey locust, osage orange, cherry, dogwood, red haw, and crab-apple, being especially intolerant of shading, cannot grow in close competition with climax species, and they become established only in fairly open situations. Their presence in thick woodland, along with climax competitors, usually is an indication that the woodland is either of recent origin or has been much disturbed in the past, permitting invasion by them.

About 1934 when approximately half of the Reservation, including nearly all the woodland areas, was fenced against livestock, shrubs and young trees sprang up in great abundance, especially in more open woodland situations, and at the edge of the forest. Sumac (*Rhus glabra*) often dominated at first in such situations. Crab-apple, wild plum, red haw, chinquapin oak, prickly ash, dogwood, honey locust, and redbud also soon came into prominence. By 1954 thickets had grown up and the intense competition had killed much of the woody vegetation. Sumac, especially, had been almost entirely killed out by the shading. By then, however, the adjacent fields had been protected for eight years from grazing, and sparse sumac thickets were present on the field sides of the fences, the average sizes of the plants progressively declining farther from the edge of the woods. Much mortality had occurred also in all the other species mentioned, with only a few of the larger surviving in competition with elm, hackberry, ash and osage orange, and with reproduction practically stopped except near the edges of the thickets.

In 1954, after approximately 20 years of protection from livestock, the woodland had become much denser, with a thick understory of saplings and tall shrubs in most places. From a time soon after protection was initiated, there was little or no reproduction (except where the woodland originally was open) in blackjack oak, dwarf or chinquapin oak, red haw, honey locust, and osage orange. On one south slope, an open woods with well scattered trees of black oak, American elm, hackberry, honey locust and osage orange, had by 1954 become so dense that it was almost impassable except with the aid of a brush knife to cut or break through the thickets. Saplings of honey locust made up an important part of the understory vegetation on this slope. Those of the smallest size group, up to 1½ inches stem diameter, were mostly dead; in a strip 900 feet long and 50 feet wide there were 29 dead saplings and ten live ones of this size group. In the next largest size group, up to 2½ inches in stem diameter, there were 17 dead and 53 live saplings, while in the size group 2½ to 3½ inches stem diameter, there was one dead sapling and 51 were alive.

On another south slope, which had more large and medium-sized trees and less dense underbrush, 233 saplings six inches or less in stem diameter, counted on a sample strip 530 feet long and 40 feet wide, included elm 37.3%, dogwood 19.7%, hackberry 16.4%, coffee-tree 15.6%, honey locust 11.0%, plum 10.3%, chestnut oak 5.5%, crab-apple 3.4%, osage orange 2.1%, red haw 1.4%, hickory, redbud, mulberry and cockspur thorn each .7%. There was substantial mortality in the saplings of several of these species; plum 86.5%, dogwood 69.5%, elm 49.5%, locust 31.2%, chestnut oak 25.0%, coffee-tree 4.4%.

By 1954 several areas of hilltop-edge and north slope, which presumably had been wooded originally, but which had been subjected to heavy cutting, supported thriving stands of young hickories mostly two to six inches in trunk diameter. Most of these saplings seemed to have originated as stump- or root-sprouts. These numerous and closely spaced saplings produced a dense and almost continuous leaf canopy, shading and killing out many of the smaller trees of their own species as well as competing elms, redbuds, dogwoods, hackberries and others.

On a north slope in the southeastern part of the Reservation, many large stumps were found in late stages of decay, cut from 20 to 30 or more years before. Insofar as could be determined, these old stumps were mostly of oaks, but in 1954 the trees growing on this slope were chiefly elms and coffee-trees less than one foot in diameter.

Effects of Livestock

Livestock importantly affected the trend of succession. The tendency of grazing animals to hold back the forest by stripping the foliage from young trees and killing them is selective, however; the several kinds of trees differ in their tolerance to browsing and in their palatability to animals. The kind of animal and the season and intensity of use also have important bearing on the ultimate effect. Several kinds of shrubs and small trees seem to be especially susceptible to damage by browsing; chinquapin oak, crab-apple, plum, hazel, dogwood, prickly ash, and paw paw were found to be either absent entirely from the parts of the woodland that were heavily used by stock, or much scarcer than they were on adjacent unbrowsed areas. Some woody plants that are even more susceptible may have been completely eliminated by browsing.

In the thirties when most of the woodland area was fenced off and protected from grazing, three wooded hillside areas of a few acres each, were maintained as connecting strips between the pastures of the hilltops and those of the bottomlands. These areas were utilized only at certain seasons, but by 1948 the effect of trampling and heavy browsing by livestock was conspicuous. Herbaceous ground vegetation was almost lacking and low woody vegetation was also scarce, in contrast to the parts of the woodland that were adjacent but separated by fences that excluded livestock. The contrast was perhaps heightened along the fences because the animals tended to follow along the fence lines and their effects were concentrated there.

In 1954 ten-foot wide strips were sampled on both sides of the fences. For both browsed and unbrowsed samples, the strips had a total length of 4000 feet, each representing an area of .919 acres. Table 4 contrasts the number of young trees per acre on the browsed and unbrowsed areas, grouped in several size classes. In general the saplings up to one-fourth inch in diameter were those that had become established in the five growing seasons since browsing was discontinued and both areas were protected. For this size group the numbers were approximately equal, being slightly higher on the browsed strips. However, in the size group of ½ inch to 4 inches in stem diameter, the trees were nearly three times as abundant on the unbrowsed areas, and most trees within this size range must have become established within the time of differing treatments. The disparity in numbers was great for hackberry, redbud, elm and dogwood which made up the bulk of the saplings. In the size range 5 to 12 inches most trees antedated the fence, and the unbrowsed portion had only a few more than the portion that had been browsed.

Table 4.—Numbers of Young Trees of Various Kinds and Sizes in 1954 on a .919-acre Area Consisting of Six Hillside Strips Each 20 Feet Wide. Each Strip Was Equally Divided by a Fence Line, Excluding Livestock from One Side During the Period 1934 (Approximately) to 1948.

	Less than ½-inch stem diameter		½-inch to 4-inch stem diameter		5-inch to 12-inch stem diameter	
	Total number	Percentage in browsed half	Total number	Percentage in browsed half	Total number	Percentage in browsed half
Dogwood	556	52.1	1058	16.4	....	....
Redbud	40	42.5	102	5.9	....	....
Elm	30	76.7	189	27.6	99	47.5
Hackberry	131	39.7	206	13.1	5	20.0
Plum	26	77.0	35	22.8	1	100.0
Crab-apple	11	100.0	46	37.0	....	....
Red haw	1	100.0	33	48.5	9	75.8
Walnut	7	28.6	32	43.7	26	61.5
Honey locust	2	100.0	20	15.0	11	27.3
Osage orange	1	100.0	7	57.1	2	50.0
Shagbark hickory	3	100.0	42	73.8	44	40.9
Chestnut oak	....	....	26	30.8	24	58.2
Chinquapin oak	....	....	12	100.0	1	100.0
Coffee-tree	....	....	11	18.1	8	12.5
Ailanthus	6	33.3	65	26.1	3	100.0
Black oak	....	....	5	40.0	7	16.6
American ash	21	100.0	3	33.3	....	....
Paw paw	12	....	61	27.8	....	....

On the formerly browsed areas clumps of gooseberry bushes were conspicuous and were computed to cover 3.81 per cent of the area sampled, versus 2.87 per cent on the unbrowsed area. These thorny bushes seem to be resistant to browsing, and elsewhere have been noted in abundance in woodlands heavily used by livestock. The elimination of competing undergrowth by browsers may be a factor favoring development of gooseberry clumps. The trend was just the opposite for fragrant sumac, which was computed to cover 1.94 per cent of the browsed sample versus 3.23 per cent of the unbrowsed sample. Greenbrier (*Smilax tamnoides hispida*) was most abundant on the unbrowsed strips, with seven large clumps, and 56 smaller clumps (10 stems or fewer) as contrasted with five large clumps and 32 smaller clumps on the browsed strips. There were 32 grapevines (*Vitis vulpina*) on the unbrowsed strips and only seven on those that were browsed.

Animal Associates

The invertebrates of the University of Kansas Natural History Reservation have not been intensively studied. Most of the species of vertebrates are characteristic of the deciduous forest of the eastern United States, or of the edge of woodland; relatively few kinds are characteristic of prairies.

Of birds, for example, some 23 species characteristic of the eastern deciduous forests have been found nesting on the Reservation, as have 14 additional species that are mainly eastern in their distribution but are most characteristic of forest-edge thickets, clearings, or marshy places. The ruffed grouse (*Bonasa umbellus*) and wild turkey (*Meleagris gallopavo*) are not present on the area, although they may have occurred there earlier. Other forest birds which occur in the general area, and which have been recorded from time to time on the Reservation, although they seem not to nest there, are: chuck-will's-widow (*Caprimulgus carolinensis*), scarlet tanager (*Piranga olivacea*), Acadian flycatcher (*Empidonax virescens*), veery (*Hylocichla fuscescens*), parula warbler (*Parula americana*), oven-bird (*Seiurus aurocapillus*), and orchard oriole (*Icterus spurius*). For each of these, habitat conditions on the Reservation seem to be deficient in some respect. On the other hand, the only typical prairie bird that breeds on the Reservation is the dickcissel (*Spiza americana*). Others, including the Swainson hawk (*Buteo swainsoni*), greater prairie chicken (*Tympanuchus cupido*), upland plover (*Bartramia longicauda*), western kingbird

(*Tyrannus verticalis*) and loggerhead shrike (*Lanius ludovicianus*), occur in the general area, and may even cross the Reservation at times, but they do not become established.

In the mammalian fauna, species typical of the deciduous forests include the opossum (*Didelphis marsupialis*), short-tailed shrew (*Blarina brevicauda*), eastern mole (*Scalopus aquaticus*), eastern gray squirrel (*Sciurus carolinensis*), and pine vole (*Microtus pinetorum*), but the eastern chipmunk (*Tamias striatus*) and southern flying squirrel (*Glaucomys volans*) are lacking. Also, the present fauna lacks large mammals that may have been present under original conditions: the white-tailed deer (*Odocoileus virginianus*), recorded on the area from time to time but not permanently established there, the wapiti (*Cervus americanus*), black bear (*Ursus americanus*), and bobcat (*Lynx rufus*). Other species on the area, that are characteristic of the deciduous woodlands, but that occur also far west into prairie regions, include the little short-tailed shrew (*Cryptotis parva*), raccoon (*Procyon lotor*), fox squirrel (*Sciurus niger*), white-footed mouse (*Peromyscus leucopus*), eastern woodrat (*Neotoma floridana*) and eastern cottontail. On the area, the only mammals that are sharply confined to grasslands, elsewhere as well as on the Reservation, are the plains pocket gopher (*Geomys bursarius*) and plains harvest mouse (*Reithrodontomys montanus*), both of which are rare on the area, and the hispid cotton rat (*Sigmodon hispidus*). The following species are typical of the plains, but they range eastward into the region of deciduous forests: western harvest mouse (*Reithrodontomys megalotis*), deer mouse (*Peromyscus maniculatus*), coyote (*Canis latrans*), and spotted skunk (*Spilogale putorius*). The following mammals, typical of grassland, are absent: black-tailed jack rabbit (*Lepus californicus*), black-tailed prairie dog (*Cynomys ludovicianus*), 13-lined ground squirrel (*Spermophilus tridecemlineatus*), Franklin's ground squirrel (*Spermophilus franklinii*), southern lemming-mouse (*Synaptomys cooperi*), and of course, the buffalo (*Bison bison*), and the pronghorned antelope (*Antilocapra americana*) long extinct in this part of their range.

Of amphibians and reptiles also, the majority are typical forest species, including: the American toad (*Bufo terrestris*), common tree frog (*Hyla versicolor*), brown skink (*Lygosoma laterale*), common five-lined skink (*Eumeces fasciatus*), worm snake (*Carphophis amoenus*), pilot black snake (*Elaphe obsoleta*), DeKay snake (*Storeria dekayi*), western ground snake (*Haldea valeriae*), copperhead (*Agkistrodon contortrix*), and timber rattlesnake (*Cro-

talus horridus). Other typical forest species missing from the area include the spring peeper (*Hyla crucifer*), Carolina box turtle (*Terrapene carolina*), coal skink (*Eumeces anthracinus*), and red-bellied snake (*Storeria occipitomaculata*). Of typical prairie species only the Kansas ant-eating frog (*Gastrophryne olivacea*) and the ornate box turtle (*Terrapene ornata*) are common, and, curiously, each seems to prefer a forest habitat on this area, in the absence of their closely related eastern representatives, the eastern ant-eating frog (*G. carolinensis*) and the Carolina box turtle, respectively, which usually live in forests. The plains spadefoot (*Spea bombifrons*), garden toad (*Bufo woodhousii*), Great Plains skink (*Eumeces obsoletus*), prairie skink (*Eumeces septentrionalis*), slender tantilla (*Tantilla gracilis*), prairie rat snake (*Elaphe guttata*), bull snake (*Pituophis catenifer*), and blotched king snake (*Lampropeltis calligaster*) are all scarce on the area. The plains toad (*Bufo cognatus*), collared lizard (*Crotaphytus collaris*), except for an introduced colony, plains garter snake (*Thamnophis radix*), lined snake (*Tropidoclonion lineatum*), and massassauga (*Sistrurus catenatus*) seem not to occur on the area at all.

Annotated List of Species

Juniperus virginiana.—Red cedar, the only native gymnosperm of northeastern Kansas, occurs in nearly all woodlands of the region, although individual trees are widely scattered. It has increased remarkably in the past few years. No mature cedar trees grow anywhere on the Reservation, but young trees, probably several dozen in all, are widely scattered in a variety of situations on the area. Probably in every instance the seeds have reached the area in droppings of birds. Approximately 15 miles south and a little east of the Reservation is a stand of cedars some of which are 100 to 300 years old. Near the southwest corner of the section, at the site of a former farm house there is a small grove of these trees, probably planted. These may have been the source for some of the young trees on the Reservation.

On several occasions cardinals (*Richmondena cardinalis*) were observed to have nested in the young cedars, whose thick foliage provided well sheltered nesting sites. This shelter was utilized especially in early nestings when foliage had only begun to appear on other trees and shrubs. However, two such nests in cedars, that were checked repeatedly, were eventually destroyed by predators.

Salix nigra.—Black willow is localized in the vicinity of the one small pond on the Reservation. The pond was made in 1936; at the upper end of a small valley a dirt bank 100 yards long was built across a ravine through which an intermittent creek drained. Hilltop fields draining into this ravine were then under cultivation. In the next few years heavy erosion occurred in the upland fields, and the soil carried downstream was deposited in the pond. Most of the pond was filled up with a silt flat about an acre in area. On the higher part of this silt flat a dense thicket of saplings of elm, honey locust and osage orange sprang up. On the lower, wetter part of the silt bar a willow grove grew up, dominated by S. *nigra,* with S. *eriocephala,* S. *interior* and S. *amygdaloides* in smaller numbers. By 1955 some of these trees had attained a trunk diameter of eight inches and a height of thirty feet. Elsewhere on the Reservation, willow is represented only by a few scattered trees and bushes along the two intermittent creeks. The silty soil preferred by the willow is scarce as both streams are actively eroding their channels.

The moist, silty soil beneath the willow grove is covered with a dense mat of low vegetation including giant ragweed, carpenter's square, dayflower, and rice cutgrass. Short-tailed shrews, house mice (*Mus musculus*), harvest mice and cotton rats thrive in this habitat. Red-winged blackbirds (*Agelaius phoeniceus*), yellow-billed cuckoos (*Coccyzus americanus*), red-eyed vireos (*Vireo olivaceus*), catbirds (*Dumetella carolinensis*) and Kentucky warblers (*Oporornis formosus*) use it for nesting. The high humidity and dense vegetation in this grove render it favorable habitat for recently metamorphosed frogs and toads, especially the tree frog, which is sometimes extremely abundant there in summer.

Populus deltoides.—Cottonwood is one of the less common trees on the area, but it attains a larger size than any of the other kinds. The larger of the two creeks on the Reservation is lined with mature cottonwoods along the lower part of its course. Along the smaller creek large cottonwoods are also present but they are more widely spaced. A few cottonwoods are present at well scattered points on slopes and hilltops, usually in forest edge situations or in woodland where other trees are sparse. By far the largest tree on the Reservation is a cottonwood of 15-foot circumference (Plate 1), growing on a hilltop near the south boundary of the Reservation, at the edge of woodland adjacent to a cultivated field.

The heavy rainfall of 1951 resulted in the establishment of hundreds of cottonwood seedlings, mostly in places remote from the mature trees. So far as observed, all these were in recent silt deposits. Many of them have survived the drought of 1952-1954.

Because of their great height, towering above the level of the surrounding tree-tops, cottonwoods are preferred look-out perches of certain of the larger birds, notably red-tailed hawks (*Buteo jamaicensis*), barred owls (*Strix varia*), and crows (*Corvus brachyrhynchos*). Flocks of robins (*Turdus migratorius*) and of rusty blackbirds (*Euphagus carolinus*) preparing to roost have been noted habitually to gather in the tops of tall cottonwoods. In spring, large wandering flocks of goldfinches (*Spinus tristis*) have been seen feeding on the leaf buds of cottonwoods. Baltimore orioles (*Icterus galbula*) and yellow-billed cuckoos often forage in cottonwoods. Red-bellied woodpeckers (*Centurus carolinus*) spend a disproportionately large amount of their time in cottonwoods. These woodpeckers have been observed nesting in the hollow branches on several occasions. Downy woodpeckers (*Dendrocopos pubescens*) also have been noticed foraging in cottonwoods on many occasions. Certain large isolated cottonwoods along creeks were favorite stopping places of blue jays (*Cyanocitta cristata*) which, on trips from one wooded hillside to another, usually perched briefly in the tops of these tall trees. Calling and looking about, the jays seemed to maintain contact with distant mates or members of the flocks by using these high perches. Often after a brief pause in the top of the cottonwood they flew off in a new direction.

Both woodrats and opossums have been known to utilize hollow cottonwoods as dens. Fox squirrels have been seen climbing in cottonwoods occasionally.

Juglans nigra.—Black walnut is one of the more prominent hardwoods. Under original conditions, evidently many of the larger trees were of this species. Being the most valuable timber species of the area, walnut has been subjected to heavy cutting over the past 85 years. Most of the walnut trees still present are small or medium-sized, but the species is still abundant over much of the area. Along certain hilltop edges there are groves of walnuts, growing in nearly pure stands, with an occasional elm, ash, coffee-tree or honey locust. Elsewhere walnut trees are more scattered, but are distributed throughout the woodland. Although the walnut trees growing in woods are of various sizes from those of mature size down to saplings, seedlings are to be found mainly in fields near the woodland edge. In these situations it is one of the more prominent of the woody species invading open lands. The seeds evidently are transported mainly by rodents, especially fox squirrels.

In autumn every walnut tree that is bearing nuts becomes a focal point of activity for squirrels. Over a period of weeks the squirrels concentrate their attention on the walnut crop, continuing until virtually every nut has been harvested. Walnut seems to be the one most important food source, for both the fox squirrel and the gray squirrel. Most of the nuts are stored for future use. Many buried separately and never retrieved by the squirrels, grow into new trees.

White-footed mice often store the nuts in their nests, in burrows, beneath rocks or in crevices. In summer, groves and isolated trees of walnuts are favorite haunts of the yellow-billed cuckoo, which finds concealment in the thick foliage, and probably feeds upon the tent caterpillars that commonly infest these trees.

Carya ovata.—Shagbark hickory is one of the more important hardwoods of the area. The trees are relatively small compared with the larger oaks, elms, ashes and hackberry. However, on several parts of the area this hickory is dominant. It grows mainly on north slopes and hilltops. The trees most frequently associated with it are black oak, American elm and chestnut oak. Scattered through the woodlands are occasional mature hickories of DBH 18 inches or more. However, many of the trees are six inches or less DBH and a large proportion of these have originated as stump sprouts from trees cut in the early thirties or before.

Shagbark is especially tolerant of shading. Numerous young trees and seedlings noted all were growing in dense woods of larger hickories, oaks, or mature elms. None has been found in open fields or even in edge situations. This hickory is resistant to drought; relatively few died during the drought of 1952-1954, and these were mostly small trees in crowded stands.

In parts of the woodland dominated by shagbark hickory the trees are mostly 5 to 6 inches or even smaller in trunk diameter and 20 to 30 feet high, sometimes growing in nearly pure stands, and with a leaf canopy so dense that shrubs and herbaceous vegetation are sparse.

The mast crop produced by shagbark is an important food source for both fox squirrels and gray squirrels. Both kinds of squirrels often use these hickories as sites for their stick nests. White-footed mice also store the nuts as a winter food source.

Birds which are most often seen in groves of shagbark include the yellow-billed cuckoo, tufted titmouse (*Parus bicolor*), black-capped chickadee (*P. atricapillus*), blue jay, summer tanager (*Piranga rubra*), and red-eyed vireo. The Cooper hawk (*Accipiter* *cooperii)* has been recorded nesting in this hickory. In dead trees of this species that are still standing, the interiors may decay more rapidly than the armorlike bark plates. On several occasions tufted titmice and chickadees have been recorded as nesting in such cavities.

Quercus stellata.—Post oak is relatively scarce on the Reservation. One area of approximately an acre on a south slope is dominated by it. There are several other small groves and scattered trees. All are on moderately steep south slopes in poor soil. Trees often found associated with it include red elm, chestnut oak, chinquapin oak, blackjack oak, hickory, and dogwood. It seems likely that under original conditions this species occupied about the same area as it does at present. It is not spreading, and there are few young trees anywhere on the area. In every instance the groves are limited to a rocky clay soil, and edaphic factors obviously are of major importance. Under original conditions fire was probably a limiting factor, and at the present time competition with other hardwoods may be even more important.

Quercus macrocarpa.—Less than a dozen individuals of mossy-cup oak have been noticed on the area, at well scattered points. Under original conditions, it probably grew chiefly in the bottomlands that have been completely cleared of timber for cultivation. The few now present are all on hillsides, and are medium to large trees.

Quercus Muehlenbergii.—Chestnut oak was perhaps the one most important tree species of the original climax forest on the area. Because of its slow growth, scanty seed production, and large heavy fruits with seeds lacking effective dispersal mechanisms, it has lost ground to other kinds of trees as a result of the unnatural disturbances which have occurred.

It still dominates on rocky upper slopes that have north, east or west exposures and forms nearly pure stands in limited areas. Nearly all the larger trees of this species now present have been cut one or more times and have regenerated from stump sprouts. Seedlings and young saplings of this oak are scarce even in parts of the woodland where the species is most common. It is evident that reproduction is slow, at least under present conditions. On the lower hill slopes these oaks are scarce and scattered, but some of the largest are in such situations. Chestnut oak seems to be relatively resistant to drought. In the summer of 1954 when elms, and especially black oaks of all sizes were dying in large numbers, the chestnut oaks growing among them showed little evidence of injury in mature trees and only a small percentage of mortality in saplings.

Chestnut oak has a relatively slow growth rate. In 17 that were recorded, there were, on the average, 4.59 annual rings per inch of trunk diameter. Near Pigeon Lake, Miami County, Kansas, counts were obtained from five cut in 1952 from a virgin stand in a habitat similar to that on the Reservation. The five trees had trunk diameters of 16½ to 25 inches and ranged in age from 65 to 183 years. Several still growing on the Reservation are larger and presumably are well over 100 years old.

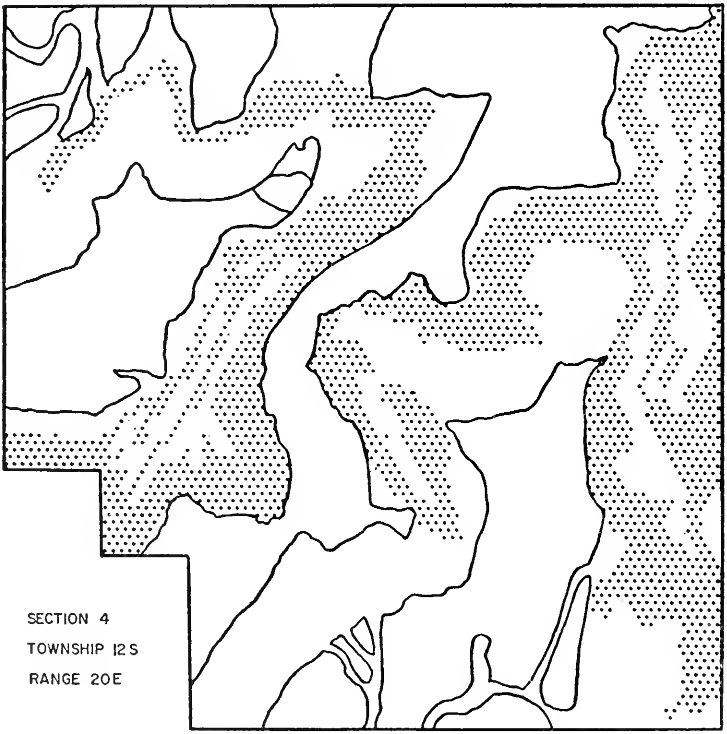

FIG. 5. Map of Reservation showing present distribution of chestnut oak (shaded). The species is not spreading and is thought to be largely confined to the area that was wooded before 1860. Except in minor details, shagbark hickory conforms to the same distribution pattern on this area.

As this oak seems to be in process of being replaced by other trees, is slow-growing, and slow in dispersal, it seems probable that the areas now occupied by its stands supported stands of it under original conditions. Whether it can regain dominance under present conditions of protection from cutting, fire and grazing remains to be seen.

The chestnut oak produces a mast crop which is utilized by many kinds of animals. Fox squirrels, gray squirrels, and white-footed mice feed upon the acorns and store them. Blue jays, red-headed woodpeckers (*Melanerpes erythrocephalus*), and red-bellied woodpeckers also eat them. The red-eyed vireo, summer tanager and tufted titmouse are among the birds that most frequently forage for insect food in chestnut oaks. Relatively few kinds of birds seem to use this tree as a nest site.

Quercus prinoides.—The chinquapin oak on this area is a small shrubby tree, usually not more than 15 feet high and more typically only six to eight feet. It occurs chiefly in dry rocky situations along hilltop edges and upper slopes, usually where the slope exposure is at least partly to the south. In such situations it may grow in nearly pure stands. Often it is associated with dogwood. The trunks are usually two to four inches in diameter, gnarled and twisted. The crowns are dense and spreading.

This oak is the dominant plant in certain small areas of its preferred habitat. In other areas of hilltop edge and upper slope it is being eliminated by stands of hickory, chestnut oak, black oak and elm, which shade it out. The species is tolerant of moderate to heavy browsing, but seemingly can be eliminated by more intensive utilization; even the higher foliage is often within reach of livestock. In "Horse Woods" one of the hillside areas that was open to livestock until 1949, this oak was almost absent, but it was abundant in adjoining parts of the woods that were fenced in the thirties to exclude livestock.

The thickets formed by this shrubby oak are frequented by cottontails, which feed upon the bark and foliage. The small acorns are used as food by rodents, especially the white-footed mouse. On several occasions, in winter, groups of long-eared owls (*Asio otus*) have been found roosting in thickets of chinquapin oak. Crows also utilize these thickets for roosting occasionally. The white-eyed vireo (*Vireo griseus*), gnatcatcher (*Polioptila caerulea*), and tufted titmouse, frequent the oak thickets.

Quercus rubra.—The red oak is one of the important climax species of the area. At present it is largely confined to a ravine in the northeastern part of the section. The woodland here is less disturbed than on most other parts of the Reservation, and red oak is the dominant species. There are large trees, rather evenly distributed, growing on east-facing and west-facing slopes. Just east of the Reservation, in the "Wall Creek" area, the small valley on either side of the creek and the adjacent lower slopes are dominated by giant red oaks larger than any now growing on the Reservation. Farther up the slope in the area of limestone outcrops, dominance shifts to chestnut oak. That red oaks of similar size, and even larger, formerly occurred on the Reservation, at least in the area still dominated by the species, is shown by the presence of a stump 49 inches in diameter, now in an advanced state of decay.

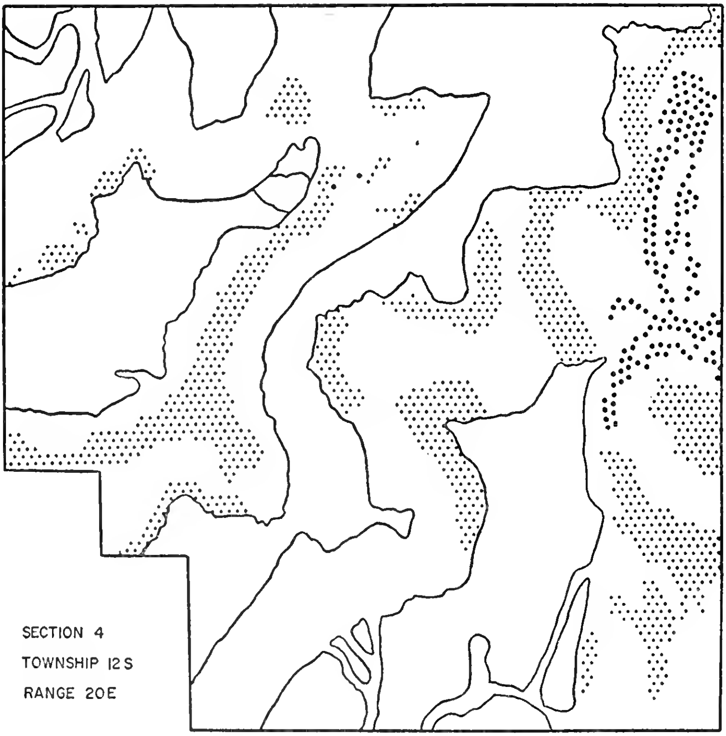

FIG. 6. Map of Reservation showing present distribution of black oak (smaller dots) and red oak (larger dots). Neither species is spreading and both are thought to be largely confined to the area that was wooded before 1860.

The large acorns of the red oak are a favorite food of the gray squirrel, which is most numerous on the parts of the Reservation where these trees are present. The red-headed woodpecker on the area tends to concentrate its activities where there are red oaks.

The fox squirrel, white-footed mouse, and blue jay are important consumers of the acorns of red oak. A pair of barred owls resided in the deep woods formed by these oaks and the associated trees.

Quercus velutina.—Black oak is one of the dominant species of the original forest climax, and is still one of the more important trees of the woodland. Like chestnut oak it shows little tendency to spread beyond its present limits. Wherever there are small trees there are old mature trees or remains of them nearby. For this reason the present distribution of black oak on the area is thought to fall entirely within the area occupied by the original forest. At present it occurs throughout most of the woodland except in the warmer and drier situations, such as on south slopes. In some hilltop situations it is common, with occasional large mature trees. In some parts of the bottomland and lower slopes it is abundant also, but there are scarcely any on the upper dry rocky slopes that are the preferred habitat of chestnut oak.

Growth in the black oak is somewhat more rapid than in the chestnut oak, as the black oak usually grows on better soil. For 15 the average growth amounted to 3.21 annual rings per inch of trunk diameter.

In 1954 a study of annual rings in a large, long dead, black oak at the bottom of a north slope near the Reservation headquarters showed that the tree was 96 years old, and hence was growing before the area was settled. Within the period of this study black oak underwent reduction in numbers more severe than that noted in any other species of tree on the Reservation. The effect of drought may have been the primary factor, although undoubtedly disease was involved also. In 1953, the second successive drought year, mortality was noticeable. Precipitation continued below normal until August 1954. By then the oaks had been decimated. On a sample strip of hilltop where 29 were recorded, 21 had recently succumbed, and their leaves were dry and withered; two were dying, though still having some green foliage, and only six were surviving. all evidently in critical condition. The mortality included trees of all sizes, even the largest and oldest. No further mortality was noted in 1955 when precipitation was only slightly below normal. On the Reservation there are many old logs, and snags still standing, of mature black oaks long dead. Earlier drought periods such as those of 1936-37 and 1925-26 possibly were also times of unusually heavy mortality. In any case it seems clear that this oak was originally more prominent in the woodlands than it is at present, and has been steadily losing ground. Even where the mature trees remain in greatest numbers the saplings are relatively scarce as compared with those of elm, ash, hackberry, and hickory. The westernmost limits of the range are nearly 100 miles west of the Reservation.

Black oak provides a mast crop which is utilized by various small mammals, notably squirrels and white-footed mice. Gray squirrels have often been noticed in or about these trees. Hairy woodpeckers (*Dendrocopos villosus*), black and white warblers (*Mniotilta varia*), and brown creepers (*Certhia familiaris*) have often been noticed foraging on the trunks. Blue jays, myrtle warblers (*Dendroica coronata*), tufted titmice, and summer tanagers frequently forage through the crowns. Often black oak trunks are hollow and the cavities are utilized by various birds and mammals including the screech owl (*Otus asio*), barred owl, raccoon, opossum, fox squirrel, gray squirrel, woodrat, and white-footed mouse.

Quercus marilandica.—Black Jack oak is localized in four small compact groves on the Reservation. These sites, though well separated, are similar. All are on steep lower slopes, where there is dry rocky clay soil and the exposure is mainly south. Probably all four groves date back to the time when the area was still in an undisturbed state. Originally they were perhaps largely separated from the remainder of the woodland. Black Jack oak is more tolerant of heat and drought than most of the other hardwoods are. The species is intolerant of fire, but perhaps was partly protected under original conditions by the sparseness of herbaceous vegetation on the poor soil where the groves were situated.

These oaks are relatively slow-growing. One stump of 9-inch diameter, typical of the larger Black Jack trees, had approximately 60 annual rings. Under present conditions there is little or no reproduction and these trees are dying out as a result of competition by other hardwoods. Under protection from fire and browsing, elms, other oaks, locust and dogwood have closed in about the groves and seem to be shading them out.

There are several mature oaks of anomalous appearance, in different places within a few hundred feet at most of the groves of Black Jack. Most of these appear to be hybrids between the present species and *Q. velutina,* as they are somewhat intermediate in size, bark texture, and leaves.

This oak produces a mast crop used by various birds and mammals, and groves are frequented by blue jays, fox squirrels, white-footed mice and woodrats. In the mid-forties when the woodrat population was high, there were many of the rats' stick houses in the groves, built either at the bases of the trunks or among the dense branchlets in tops of fallen trees. By 1952 the population of woodrats was much reduced and had disappeared entirely from these groves. The houses were collapsed and decaying.

Horned owls (*Bubo virginianus*) and barred owls often make their day roosts among the dense interlacing twigs of these trees, and red-tailed hawks have been known to roost for the night in the same kinds of situations.

Ulmus americana.—On most parts of the area American elm is the dominant tree. It occurs throughout the woodland, and most of the larger trees are of this species. In each of the fields that were formerly cultivated, and in the pasture areas, there are many saplings. More than one hundred elms of DBH two feet or more have been recorded. Presumably these mostly date back 90 years or more and were already growing on the area when it was relatively undisturbed. On the area the distribution of these large elms corresponds in a general way with the present distribution of the oak-hickory type. The coinciding distribution of the climax species and of the largest trees is believed to reflect the distribution pattern of the original forest, except that clearing was thorough in the bottomlands so that hardly any trees of the climax species, or large trees of any kind remain. Several elms of three feet or more DBH were recorded, and the largest one measured was 46 inches. The largest elms are in alluvial soil near small creeks in the two valleys. Also many large elms grow along the upper slopes, especially along the outcrops of the two main strata of the Oread Limestone. Such sites along the outcrops on open slopes are the first to be invaded. The rock strata are relatively impervious to water, which is held at a depth where it is readily available to the trees. Along rocky upper slopes between the two outcrops, where chestnut oak is abundant, elms are relatively scarce and seem unable to compete successfully. It is noteworthy that elm is not mentioned in several of the descriptions (Taft, 1950; Parks, 1854; Robinson, 1899) of the original forest, even in listings of the species present. It must have been much less prominent until favored by disturbed conditions.

In July and August, 1954, a large proportion of the elms on the area died. The die-off included trees of all sizes, and evidently the cumulative effect of drought in 1952 and 1953, continuing into the spring and summer of 1954, was the primary cause, although diseases such as phloem necrosis, and insect infestations, may have intensified its effect. In August of 1954 the bare dead elms stood out conspicuously in the mass of green foliage surrounding them. Most of them had survived the two dry summers of 1952 and 1953 with little evident loss in vitality. However, the continued lack of moisture as the 1954 growing season progressed, and the extremely hot weather of June and July caused heavy mortality. In the course of a few days the foliage of the upper branches would wither, die and turn brown. In some instances numerous sucker shoots grew from the trunk of the tree as the top was dying. Mortality was especially heavy on south-facing slopes. Certain ecologists believe that over the years, as trees deplete subsoil moisture and

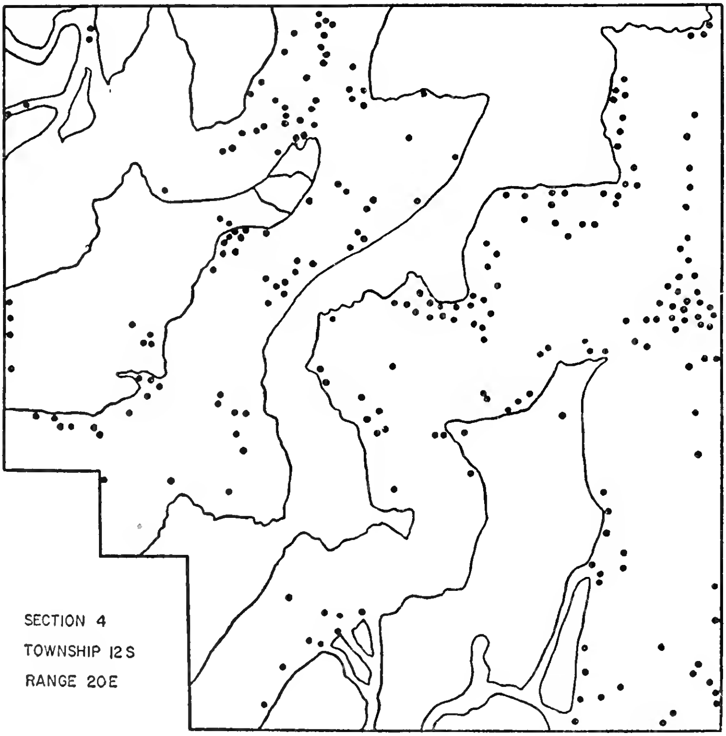

FIG. 7. Map of Reservation showing present distribution of the largest American elms, those more than two feet in trunk diameter. American elm is increasing and spreading on the area, and smaller trees are abundant even in former cultivated fields and pastures. Growth rate varies according to site, but these larger trees are, in many instances, 90 years or more in age and most of them are thought to be in the area wooded in the eighteen sixties and before.

periodic droughts make their effects felt, other species also will die off and eventually prairie will replace them where the present forests are growing in dry and exposed situations.

Infestations of the introduced bark beetle, *Scolytus multistriatus*, were common and probably contributed to death of many elms. In the winter of 1953-54 before much mortality had occurred, the bark beetle infestations had become conspicuous. Especially on south slopes elms of about six inches DBH were heavily infested. Woodpeckers, including the downy, hairy, and red-bellied, habitually resorted to the elm trunks to forage. As a result of their activities chips of bark accumulated sometimes to a depth of several inches around the bases of the trunks, and the exposed inner layers of brown bark caused the infested trees to contrast with the predominantly gray color of those that were still healthy and retained the outer layer of bark.

In April and early May seeds of the American elm constitute a major food source for birds, including the black-capped chickadee, tufted titmouse, junco (*Junco hyemalis*), red-eyed towhee (*Pipilo erythrophthalmus*), Harris sparrow (*Zonotrichia querula*), cardinal, goldfinch, tree sparrow (*Spizella arborea*) and field sparrow (*S. pusilla*). Birds recorded as nesting in the American elm include the mourning dove (*Zenaidura macroura*), Cooper hawk, red-tailed hawk, broad-winged hawk (*Buteo platypterus*), turkey vulture (*Cathartes aura*), screech owl, horned owl, barred owl, red-bellied woodpecker, downy woodpecker, tufted titmouse, black-capped chickadee, gnatcatcher, red-eyed vireo, summer tanager, indigo bunting (*Passerina cyanea*), field sparrow and cardinal.

Opossums, raccoons, fox squirrels and white-footed mice often live in cavities in elms.

Insectivorous birds that find their food on foliage and prefer elm or use it to a large extent are: yellow-billed cuckoo, tufted titmouse, black-capped chickadee, blue-gray gnatcatcher, red-eyed vireo, white-eyed vireo and warblers, including the myrtle, Audubon (*Dendroica auduboni*), yellow (*D. petechia*), black-throated green (*D. virens*), black-poll (*D. striata*), Tennessee (*Vermivora peregrina*), orange-crowned (*V. celata*), Nashville (*V. ruficapilla*) and American redstart (*Setophaga ruticilla*).

Ulmus rubra.—The red elm (or slippery elm) is widely distributed over the area, but only a few trees with a trunk diameter of twelve inches or more are present. Throughout the woodlands of the Reservation the saplings of this species constitute a prominent part of the understory. However, few survive beyond the sapling stage. The red elm is never abundant in Kansas woodlands. It is intolerant of drought conditions, and is one of the first trees to die. This fact probably explains the scarcity of mature trees of this species on the Reservation.

Celtis occidentalis.—Hackberry is widely distributed on the area, but is not dominant anywhere. Its favorite site is along hilltop limestone outcrops, especially where there is south exposure. There are few on hilltops away from the outcrops. Hackberries are scattered in small numbers over the wooded slopes. There are a few of unusually large size, along edges of the bottomlands. Hackberries are slow-growing. Counts of annual rings for four indicated an average of 7.1 rings per inch of trunk diameter. Young hackberries of all sizes are numerous throughout the woodland. Therefore it seems likely that this species is in process of spreading and probably has already extended beyond the situations which it originally occupied.

The fruits of hackberry provide a fall and winter food supply for various animals. Opossums are especially fond of them. Red-bellied woodpeckers have been seen storing them. Migrating flocks of robins may utilize them as a major food source temporarily. White-footed mice and woodrats store them and eat them.

Morus rubra.—Red mulberry is moderately common in certain heavily wooded areas, especially the lower parts of north slopes. A few are present on wooded hilltops. Most of the trees are between ten and twenty feet tall, and generally die before growing larger. Red mulberry is present in most woodlands of eastern Kansas and is seemingly distributed by birds. It is never an important component of woodlands in the area. Catbirds (*Dumetella carolinensis*) and wood thrushes (*Hylocichla mustelina*) especially have been noted frequenting the vicinity of mulberry trees in fruit. Probably many other kinds of birds utilize the fruits to some extent.

Maclura pomifera.—Osage orange was not a member of the original flora, but early settlers in Kansas valued it for windbreaks and fence posts, and they made extensive plantings. Presumably it was introduced onto the area of the present study in the eighteen sixties. At the present time it occurs throughout the woodland, with scattered mature trees and many young trees on the former pastures. This aggressive invader spread despite frequent cutting, and now plays an important part in the ecology of the area. Most of the larger trees have been cut one or more times, but have regenerated from stump sprouts with multiple stems and spreading habit. The tough and durable wood is useful for fence posts. The growth rate is slow, similar to that of oaks and elms.

Osage orange is intolerant of fire and is easily killed by scorching. It is damaged by browsing, and cannot grow in deep shade. It is drought resistant. Mortality was light during the drought period of 1952-1954, although many of the trees were growing on poor soil in the hotter and drier sites.

Where there are stands of mixed hardwoods, osage orange is relatively scarce and tends to be on or near the edges of the stands. The osage orange trees growing in competition with oaks, elms and hickories may have tall, slender trunks and narrow crowns, in contrast with the spreading habit of those growing in more open sites. In the woodlands small and medium-sized trees are scarce and there is hardly any reproduction. Obviously the osage orange, like honey locust became established in the forests when the stands were more open, probably after cutting of the large trees. In contrast to the meager reproduction in shaded sites is the abundant crop of young saplings along edges of fields adjacent to woods or about isolated osage orange trees. Evidently the tree does not become established readily on bluestem prairie. On a hillside adjoining the northwest corner of the Reservation, long subjected to heavy grazing, osage orange dominates, but just across the fence on the Reservation side, it is almost absent. This area had been maintained as bluestem prairie until about 1934 by occasional burning and since then had partly grown up into thickets in which dogwood, and saplings of elm and hackberry were abundant.

The dense thorny branches provide shelter and nesting sites for many kinds of animals. On this area the cardinal utilizes it for nesting sites more frequently than any other kind of tree. Some nests were so well protected by the thorns that they could scarcely be reached. Indigo buntings, field sparrows, and yellow-billed cuckoos also use these trees or young saplings for nesting sites.

In the forties, when the woodrat was common on the area, its local distribution seemed to be determined mainly by the osage orange. Many houses of the woodrat were built around old stumps at the bases of large, spreading osage orange trees. Frequently the houses were in the main crotch of a tree two to eight feet from the ground. Characteristically the rats used horizontal or gently inclined, low branches of the tree as runways to and from the house. In summer and early autumn these rats stored foliage of the osage orange in large quantities in chambers adjacent to the nest. The seeds also provided an important food source. During the period 1948 to 1951 the woodrat population steadily decreased, and one by one the houses in osage orange trees were deserted, until the small surviving population of woodrats was limited to hilltop rock outcrops not associated with osage orange trees.

The seeds are well liked by other rodents also. In late fall and winter after the "hedge balls" have fallen, fox squirrels visit the trees and shred the fruits to gain access to the seeds. Over periods of weeks heaps of the shredded refuse accumulate at the base of the tree trunk. The seeds probably constitute the one most important winter food of the fox squirrel. The tufted titmouse also relies to a large extent on the seeds for its winter food. Being unable to shred the bulky hedge balls itself, it depends almost entirely on the seeds in fruits torn open by the squirrel but not fully utilized by it. At times when the ground and trees are snow-covered, making unavailable most other food sources, the osage orange seeds gleaned from refuse heaps in the sheltered feeding places of the squirrels are probably of critical importance to the titmouse.

The cottontail and white-footed mouse also eat the seeds.

Platanus occidentalis.—Sycamores are few and scattered on the area, but those present seem to be holding their own if not gaining in numbers. They include some of the largest trees on the Reservation. The most typical habitat is along rocky ravines on wooded slopes. Occasional trees are scattered through the woods away from ravines on slopes of north, east, or west exposures, or on hilltop edges, providing strong evidence that these areas were more open at the time the sycamore seedlings became established. Cutting of the mature trees in the original forest and subsequent grazing might have created the conditions favorable for their establishment. Many saplings have sprung up in the fallow hilltop fields that were formerly cultivated.

Many of the larger sycamores have cavities and these are inhabited by various animals. A large sycamore in a ravine below a pond had a cavity in its base within which a raccoon reared its litter of young one summer. At other times this same cavity was inhabited by woodrats and by fox squirrels. Seemingly this cavity was the habitat of a certain chigger which was found on both the squirrels and the woodrat. Red-bellied woodpeckers excavated a cavity high on this same tree trunk, in which they reared their brood.

Several large sycamores died as a result of the cumulative effect of drought in the summers of 1952, 1953 and 1954, but many others survived.

Prunus americana.—Wild plum is a small tree, usually not more than three inches in trunk diameter, nor more than twelve feet high. It tends to grow in dense thickets which are spotty in distribution. Several of these thickets are in edges of former pastures at the woodland edge. Other extensive thickets are in the following situations: along hilltop rock ledges and encroaching into adjacent prairie on upper south-facing slope maintained as bluestem prairie by mowing and burning, until 1934; along a ravine in formerly cultivated hilltop fields; along tops of steep creek banks at edge of old corn field. In a few situations within the woodland there are dead and dying thickets of wild plum, shaded out by the closing in of the tree canopy, as fast-growing trees such as elm, honey locust, and cherry sprang up in former clearings.

The woodrat lived in several plum thickets that provided the type of shelter from predators that it requires. The bark, fruit and foliage are used as food. In autumn the plums sometimes are the chief food of the opossum. Plum thickets provide the preferred habitat for the Bell vireo (*Vireo bellii*). The white-eyed vireo, field sparrow, tree sparrow, Harris sparrow, and white-throated sparrow (*Zonotrichia albicollis*) also frequently use these thickets.

Prunus serotina.—Isolated trees of black cherry six to fifteen inches in trunk diameter, have been noted on various parts of the Reservation at widely scattered points. On a flat hilltop at the southeastern corner of the Reservation there are many large trees of black cherry, which make up a major portion of the stand, and trunks of some are as much as 21 inches in diameter. Other trees in the vicinity are mostly elms and honey locusts, and seemingly the area was more open or perhaps entirely treeless in the recent past. The presence of black cherry in forest often can be interpreted as indicating more open conditions at the time the seedling became established. Black cherry prefers a rich soil and an open habitat; hence it is generally not common in woodlands of northeastern Kansas.

The fruits of black cherry are a favorite food of the opossum, and the seeds have often been noticed in the scats of this animal. White-footed mice store and eat the seeds. Two trees of black cherry well isolated from other trees except for saplings in low thickets, constituted the headquarters of a Bell vireo's territory each summer from 1951 through 1955.

Pyrus ioensis.—Crab-apple is a small tree, usually less than five inches in trunk diameter and less than 12 feet high. It grows both in woodlands and in former pastures, but chiefly along the line of contact. After removal of livestock in early 1949, crab-apple spread into the edges of hilltop pastures, from the adjacent protected woodland. Each year thickets of encroaching crab-apple have extended farther into the fields, until, in 1955, there were graded series from the trees along the fence, six feet high or more, to the seedlings 30 to 50 feet out in the fields. Dogwood, red haw, and smooth sumac are among the most common associates of crab-apple as they share its tendency to invade open land adjacent to the forest.

Evidently the tree is intolerant of browsing by livestock, as few were growing in the pastured areas in 1948, but as soon as livestock were removed these areas were rapidly invaded.

The thickets formed by crab-apple provide shelter for many kinds of animals. Cottontails, especially, tend to stay in or near these thickets. In autumn the fruits are eaten by them, and in winter, when the ground is covered with snow, the bark is a major food source. Most mature or partly grown trees show old scars near their bases, where the rabbits have attacked them. Often the trees are completely girdled. In years when snow lies on the ground for long periods girdling is extensive and a substantial portion of the trees in the thickets may be killed, but this mortality has been insufficient to check the rapid spread of crab-apple.

The crab-apple is one of the trees preferred as a nesting site by the cardinal. Other birds that frequently use the crab-apple tree as a nest site include the field sparrow, towhee and indigo bunting. White-footed mice, prairie voles and pine voles eat the fruit and seed.

Crataegus mollis.—Red haw occurs over much of the Reservation, both in woodland and former pastures. The trees are scattered, and are not dominant, even on small areas. In the woodland, haw usually grows in the more open situations. Where there are haws in denser woods, they are usually large and old; seemingly they are survivors from a time when the woods were more open. Haw is intolerant of shading, and being of lesser height than any of the climax species, it cannot compete with them. The present wide distribution of haw on the area is secondary, resulting from the extensive cutting of the larger trees and opening up of the woodland. Haw trees are most numerous on south facing slopes that have grown up into thickets in the last 30 years. Here its associates are chiefly honey locust, osage orange, dogwood and elm.

Red haws have been recorded as nest trees of horned owls, yellow-billed cuckoos, cardinals, and fox squirrels. Cavities in the trunks are used by downy woodpeckers, titmice, chickadees and white-footed mice.

Cercis canadensis.—Redbud is abundant in some parts of the woodland. Trees are up to nine inches in diameter and 25 feet high. They grow chiefly in rich soil on hillsides in moist situations. Redbud and dogwood are in part complementary in distribution, each forming an understory in parts of the woodland where the leaf canopy of larger trees is not too dense. However, redbud is more tolerant of shade. In general dogwood grows in the drier, more rocky situations and redbud in better soil and damper sites. In the southeastern part of the Reservation, on a west facing slope, redbud dominates, with smaller numbers of elm, blackjack oak, and dogwood.

Several times nests of yellow-billed cuckoos were found in redbuds. Titmice, chickadees, and red-eyed vireos forage in redbuds on many occasions. Brown creepers forage on the trunks. Titmice, chickadees, and downy woodpeckers used cavities in dead or dying redbuds. However, there is no evidence that this tree is especially attractive to any kind of vertebrate, or plays an important part in the ecology of the area.

Gymnocladus dioica.—Kentucky coffee-tree is one of the less important trees on the area but it is widely distributed. In general it is absent from the denser woods. On limited areas of certain slopes it is the dominant species. The groves sometimes are in nearly pure stands. Slope exposure evidently is not the determining factor in the local distribution as groves have been found on hillsides of varying exposure. The tree seems to flourish where the forest has been opened by cutting of the larger trees. Groves are mainly on the more gently sloping parts of the hillsides, or on the nearly level terrace. There are few coffee-trees more than 12 inches in trunk diameter. The largest tree examined was 27 inches.

In May, groups of orchard orioles (*Icterus spurius*) have been observed in coffee-trees, seemingly attracted by the blossoms. These concentrations never lasted more than a few days and seemed to involve individuals that were still migrating or newly arrived and not yet established on their territories.

In winter the large pods of this tree are used as food to a limited extent by cottontails. The large hard shelled seeds resist attack by most animals. Seemingly they are used by white-footed mice, as they have often been found stored in the nest cavities of these mice, beneath rocks or in logs.

Gleditsia triacanthos.—Honey locust is at present one of the more important species of trees on the area. There are scattered locusts throughout most parts of the woodland. In the bottomland fields there are groves and scattered trees of medium to large size. On south slopes honey locust, osage orange and red elm form thickets. On hilltops, along woodland edges where fences were installed in the mid-thirties, young honey locusts have become established and are now abundant. Some have grown to a diameter of 8 inches or more. Honey locust is the fastest growing of the trees on the area and therefore has an early advantage in competing with other kinds. A locust of 25-inch diameter cut in 1950 was found to have 32 annual rings, an average of only 1.3 rings per inch as contrasted with an average of 3.8 for all the trees studied, and more than 9 for some of the slowest growing. In open fields, both those used for pasture and those formerly cultivated, young honey locusts have sprung up in abundance since the discontinuance of grazing in 1948. The species is resistant to drought. It seems to have been limited on the area mainly by grazing and shading. The locusts growing in the woods tend to be concentrated near its edges. Those that are deeper in woodland evidently became established after heavy tree-cutting had opened clearings. Locusts in such situations, competing with other hardwoods are of much different form than those growing in the open; the trunks are long and slender and the crowns are narrow.

The south slopes that were originally prairie, were evidently only sparsely clothed with trees up until the thirties when livestock were fenced out. Then the abundant growth of shrubs and young trees formed thickets. Honey locust, growing rapidly tended to dominate. The younger locust saplings that were shaded beneath the leaf canopy died in large numbers.

Honey locust plays an important part in the over-all ecology of the area, providing both food and shelter for many kinds of animals. The foliage is well liked by livestock; consequently young trees have little chance of surviving in heavily grazed pastures. Rabbits like both the foliage, and the bark. Often they girdle or injure young trees, and eat the beans. Both the prairie vole and the pine vole often feed upon the inner bark and root crowns of small saplings, sometimes completely undermining them. These voles also store and eat the seeds. Beneath large mature locusts, runway systems and burrows of the pine vole are sometimes much in evidence. As ground vegetation is scanty in these places it seems that the voles are attracted by the abundant supply of locust seeds.

The spiny branches of locusts provide well protected nesting sites that are utilized by various kinds of birds; mourning dove, horned owl, yellow-billed cuckoo, gnatcatcher, cardinal and goldfinch have been recorded nesting in locusts. The wood is relatively soft. The hairy woodpecker has been recorded nesting in a cavity which it had dug in a living honey locust, while the black-capped chickadee and red-bellied woodpecker have been recorded nesting in cavities in dead limbs. The summer tanager prefers large locusts near the edge of woodland as singing stations.

Fox squirrels also often exploit the spiny protection provided by locust trunks, and build their stick nests in these trees, usually in a fork of the main trunk eight to twelve feet above the ground. Such nest trees often are either isolated or are in groves of other locusts. Presumably the squirrels are attracted to them by the supply of locust seeds.

Acer Negundo.—Boxelder probably was not a part of the original flora of the Reservation. The trees present now are few and scattered, and most are not more than eight inches in trunk diameter. The species seems intolerant of shade and does not grow in the denser woodlands. A few are present along the banks of the intermittent streams, and there are others in open woodlands of south slopes. The small patch of bluestem prairie remaining at the northwest corner of the Reservation is being invaded by a variety of shrubs and saplings, and boxelder is by far the most prominent of these invaders, with two hundred seedlings and saplings per acre.

Ailanthus altissima.—Tree-of-heaven is an Asiatic species that was introduced early into northeastern Kansas, and has become established locally in the woodland. Most of those on the Reservation are near the central part of the southwestern one-fourth. Concentrated about the site of an old homestead, occupied in the eighteen-seventies, within a few acres, there are dozens of mature trees, up to 22 inches in trunk diameter, and hundreds of saplings. Elsewhere on the Reservation the species is scarce and is represented by isolated trees and scattered clumps at a few places.

Cornus Drummondi.—This dogwood is the most abundant tree on the area. However, it scarcely reaches the size of a tree. Most mature examples are 1½ to 3½ inches in trunk diameter, and rarely more than twelve feet high. Dogwood grows in greatest abun-

EXPLANATION OF PLATE 7

Upper figure shows gully in southeastern part of Reservation, which has enlarged and deepened greatly in the past 40 years. Heavy precipitation in the summer of 1951 resulted in the undermining and collapse of many large and medium sized trees, as shown in this photograph taken in March, 1956, by H. S. Fitch.

Lower figure shows cottonwood fifteen feet in circumference, growing on hilltop near south edge of the Reservation. This is the largest tree on the area. Several exceptionally large black oaks, chestnut oaks, and elms are present on the same hilltop. Photograph taken in December, 1954, by H. S. Fitch.

PLATE 8

Large American elm at edge of bottomland field in west part of the Reservation. Photograph taken on April 2, 1955, by H. S. Fitch.

dance on dry rocky slopes where other trees are scarce. In small areas it may be the dominant tree, often closely associated with chinquapin oak and red elm. In parts of the woodland where there are larger trees, dogwood may form an understory, its development depending largely on the amount of light passing through the upper leaf canopy. Where the canopy is dense and nearly continuous, dogwood tends to be eliminated by shading. In some situations where forest has recently closed in, most of the dogwoods are dead or dying. Especially on formerly cut-over north slopes, where oak and hickory have sprung up in a dense stand 20 feet high, with a thick canopy, most of the dogwoods have been eliminated.

On the remaining hillside prairie near the northwest corner of the Reservation, dogwood is the most prominent of the trees and shrubs encroaching onto the area since it has been protected from fire—a period of approximately 20 years. There are dense thickets of dogwood along the borders of the prairie and the woodland edge.

The white-eyed vireo and Bell vireo both forage and nest in thickets of dogwood and other shrubs.

Fraxinus americana.—White ash is localized on the Reservation and most of the mature trees are within an area of perhaps three acres on a steep slope of northwest exposure. Several of the largest trees, well over a foot in trunk diameter, grow at the lower limestone outcrop. Ash is most abundant at this level and at the terrace just below it. On the one slope where it is concentrated, ash is one of the most common trees, growing in association with American elm, chestnut oak, black oak, and shagbark hickory. This area is one of the most mesic on the Reservation. The soil is usually damp, with thick leaf litter and rich humus. In hilltop fields, formerly cultivated or pastured, saplings of white ash are among the most prominent invaders.

The leaves of this tree and especially its saplings, are favorite foraging places for the tree frog. The groves of this tree provide favorable habitat for the opossum, short-tailed shrew, gray squirrel, and white-footed mouse. Birds that frequent the same habitat include the black-capped chickadee, tufted titmouse, blue jay, rose-breasted grosbeak (*Pheucticus ludovicianus*), yellow-billed cuckoo, red-eyed vireo, gnatcatcher, hairy woodpecker, Kentucky warbler, and crested flycatcher (*Myiarchus crinitus*).

Summary and Conclusions

The University of Kansas Natural History Reservation, in the northeastern corner of Douglas County, Kansas, is situated in an area that originally supported two types of climax vegetation, tall grass prairie, and hardwood forest. These associations were distinct and sharply defined. The present distribution of the different species of trees on the area, supplemented by the data from snails, indicates the approximate distribution of the two original climaxes. The principal climax trees of the original forest were mossy-cup oak (mainly in bottomlands), black walnut, shagbark hickory, hackberry, red oak, black oak (mainly on hillsides and hilltop edges), chestnut oak (mainly on rocky upper slopes). Subclimax trees characteristic of marginal situations include: American elm, red elm, white ash, honey locust, osage orange, coffee-tree, red haw, dogwood, redbud, cherry, wild plum and crab-apple. Others characteristic of hydroseral situations include sycamore, willow (of four species), and cottonwood.

In the Kansas River flood plain and small tributary valleys, rich mesophytic forest of predominantly oak-hickory type was present. In somewhat stunted form, and with partial replacement of its species by those of more xeric habit, it extended up onto hillsides sloping north, east or west, and onto the adjacent hilltop edges. Slopes having poor shallow soil and exposures mainly to the south supported chiefly tall grass prairie, but also had compact clumps of blackjack oak and post oak, usually more or less isolated from other parts of the woodland. Hilltops were mostly treeless (except near their edges) and supported a tall-grass prairie vegetation. Shrubs and various kinds of small trees must have been a much less conspicuous part of the woodland flora than they are at present, and occurred in small ravines where shelter was inadequate for the larger forest trees, and also along the extensive line of contact between forest and open land.

One of the earliest changes was the destruction of the bottomland forest. With the rapid settlement of the region in the sixties and seventies, lumber was in demand and the supply was limited. The cleared land was productive as pasture. Heavy grazing combined with drought, gradually altered the original tall grass prairie; the bluestems and other perennial grasses were replaced by the introduced blue grass and by various weedy forbs. Prolonged protection from fire permitted encroachment of trees and shrubs into situations where they had not grown previously. Heavy grazing however, tended to hold in check the spread of the woody vegetation.

When the bottomlands had been cut over, lumbering operations were extended onto those hillsides where the better stands of trees were located. The cutting of large, mature oaks, walnuts, and hickories opened up the woodland and permitted large scale encroachment by subclimax species. American elm, especially, sprang up in thickets. Ash, honey locust, cherry, red haw, crab-apple, dogwood, and the introduced osage orange, thrived and spread in the situations to which they were especially adapted. These species largely replaced the original climax. Some of the trees cut, the oaks, sycamores, and hickories, usually produced fast-growing stump sprouts and competed vigorously with the invaders. At each successive cutting, however, the climax species lost ground. American elm, being tremendously prolific of seed, and only a little less tolerant of shading than its climax competitors, soon became the dominant tree of the woodlands.

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Transmitted April 20, 1956.

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December 19, 1957

Aspects of Reproduction and Development in the Prairie Vole (Microtus ochrogaster)

BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
1957

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16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.

17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.

18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 10, No. 4, pp. 129-161, 8 figs. in text, 4 tables
December 19, 1957

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PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1957
26-7561

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INTRODUCTION

The prairie vole is by far the most abundant mammal on the University of Kansas Natural History Reservation and on grassland areas throughout northeastern Kansas. This vole therefore affects the vegetation, perhaps more than any other native vertebrate, and it is an important food source for most of the vertebrate predators. Since the Reservation was established, in 1948, more data have been accumulated concerning this vole than for any other species of animal there. From February, 1950, to February, 1954, a grid of live-traps at 50-foot intervals was set for several days each month in a three-acre field inhabited by voles, and the population of marked individuals was studied throughout the four-year period. From November, 1953, to June, 1956, a half-acre trap grid with 20-foot interval was used on an area adjoining the three-acre field. Other trap lines in somewhat different habitats were maintained for shorter periods as a basis for comparison. By June, 1956, a total of some 3550 voles had been caught and recorded 14,750 times in all. The present report is a preliminary attempt to analyze, in part, these extensive data, and is concerned with certain phases of the species' reproduction and growth that have bearing on the observed population changes from month to month and from year to year on the Reservation.

Through the studies of Jameson (1947) and Martin (1956), both made in the same general area as my own, and several earlier studies, the life history and ecology of the prairie vole are already well known. The present report, with much larger amounts of data, further clarifies certain phases of the ecology; and by using types of data not available to Jameson and Martin I have dealt with some topics not included in their reports.

Previous studies of growth in *Microtus* have been based almost entirely on weights. However, the weight of an individual vole may fluctuate widely over a short period, depending on pregnancy and parturition, length of time in a trap without food, availability of moisture, and other factors. In the course of my study, in 1954 and 1955, and parts of 1953 and 1956, measurements of total length, in addition to weights, were recorded for most of the voles live-trapped.

To test the accuracy of measurements, successive readings were compared in individual voles that were already of large adult size and that presumably either had stopped growing or were growing so slowly that the gain was scarcely detectable in the relatively short periods involved. For 200 such readings 33 per cent were just the same as previous records for the same animals, 24 per cent deviated by 1 mm., 22 per cent deviated by 2 mm., 15 per cent by 3 mm., 4.5 per cent by 4 mm., .5 per cent by 5 mm., 1 per cent by 6 mm., and .5 per cent by 7 mm. On the average, successive measurements varied by 1.43 mm., somewhat less than one per cent of the adult vole's total length. Occasional errors of two to four per cent were easily eliminated because for the voles used for growth records, series of measurements were available, with clearly defined trends. The occasional readings that deviated from the general trend for the individual were discarded.

Measurements were recorded along with other data in the field at the point of capture. Obtaining a reasonably accurate measurement on a live and struggling vole required patience and practice. With the thumb and forefinger of the left hand, I grasped the vole by loose skin of the nape, and simultaneously grasped the tail at a point approximately three-fourths of the distance to the tip. Then, with gentle but steady pressure, I stretched the vole out to its full length, meanwhile manipulating a millimeter ruler with the free fingers, so that the vole was pressed against it, with the nose pad at the end of the ruler.

The total length measurement is considered the best index to over-all size. The relative tail-length varies slightly between individuals, averaging approximately 22 per cent of the total length. Individuals having broken tails, or having the distal parts of their tails missing, were not included. The total length can be measured with greater accuracy than can either the head-and-body length or the tail-length separately.

GENERAL SOCIAL BEHAVIOR

As compared with other mammals, voles are tolerant and somewhat social. That individuals are not mutually exclusive (territorially) in areas occupied was demonstrated on many occasions when more than one individual was caught simultaneously in the same live-trap. Injury of a vole by a trap-mate was a rare occurrence. Multiple captures often involved a female in oestrus and one or more males, or a female and her young, but other instances involved various combinations of sex and age groups. As many as five adults have been caught in a trap simultaneously at times when the population density was high. At such times, the meadow habitat is crossed by a maze of interconnecting surface runways and one runway may be traced continuously for 100 yards or more. Because each individual vole normally confines its activity to a small area, only a fraction of an acre, it is evident that individuals living at different places overlap in their home ranges, and also in the trailways followed in foraging. A high degree of tolerance is indicated. Where population is so sparse that the systems of surface runways comprise separate and isolated units, trapping experience has shown that one such system may harbor several or many individuals.

As direct observations on voles under natural conditions are rarely feasible, because of the animals' timidity, their utilization of concealing cover, and tendency to crepuscular habits, best evidence of social habits and underground life is based upon behavior of captive individuals. Many voles were kept in confinement for varying lengths of times, either singly or in association with others. Under such conditions there was sometimes sporadic fighting, but it was mainly defensive and serious injuries were rare. Two or more voles caught at a given spot regardless of whether they were found in the same trap simultaneously, or trapped separately within a short time, usually were completely tolerant of each other. When at rest in their container, such voles would huddle together in a corner or in a nest, if materials were provided, so that collectively they presented the minimum exposed surface. The intimacy and lack of antagonism displayed on such occasions, suggested that the voles were accustomed to living together amicably in the same nest chamber. In live-trapping, "double" captures in a single trap often involved the same two individuals. Such trapmates were often male and female, and in many instances the female was not in breeding condition. That the voles are not monogamous in habits was demonstrated when the same female was often trapped in association with either of two males. Other trap associates taken together repeatedly often were two males, or two females. Voles that are nest mates or "neighbors" may tend to move about together in their foraging, or one confined in a trap may attract the other sufficiently to cause it to force an entrance by lifting the heavy door of a trap.

When a new vole, caught at a different location, is added to a container in which one or more are already confined, there is mutual circumspection between the original occupants and the newcomer. At first, each vole is intimidated by movements of the other, and as a result, the original occupants huddle in their established corner while the newcomer cowers in the most remote part of the container. Gradually the voles become less timid and one may approach another slowly and cautiously, to sniff at it. The vole approached may react with a show of hostility which is largely defensive. In the characteristic posture of threat for defense, the vole crouches, or rears back on its haunches, with snout elevated and incisors prominently displayed. If the warning posture is unheeded, or if the vole is made unusually aggressive by having young to defend, or for some other reason, it attacks with a sudden forward lunge, striking the adversary simultaneously with both forefeet and with the incisors. The lunge is so rapid that when I have observed it, I have been unable to discern whether the attacker bit its opponent. The attack serves to force back the other animal, throwing it off balance and intimidating it. The attacked animal may dodge nimbly to avoid the lunge, but whether or not it is actually struck, it usually retreats, avoiding or postponing further hostilities. Voles that have been kept in containers for periods of hours or days tend to be more hostile and aggressive toward a newcomer than are those newly introduced. After series of meetings resulting from the exploratory behavior of the newcomer and the curiosity or normal activity of those longer confined, hostility gradually subsides. Within a few hours a newcomer is usually accepted, and thenceforth he huddles with other members of the group when at rest, and hostility is rarely evident.

This ready acceptance on short acquaintance of strange voles into the family or social group suggests that lack of territoriality extends even to the use of the nest burrows, and that groups of voles may share the same nest, huddling together and deriving mutual benefit from the association, such as warmth in cold weather. Schmidt (1931: 113), studying this vole in Clark County, Wisconsin, noted its colonial habits. He found isolated small mounds that were riddled with burrows, and little sign in intervening areas. At one mound he trapped two adult males, one adult female, and two young; at another mound, two adult males, two adult females, and four young were trapped. My individuals that were released from live-traps were on many occasions trailed by means of a stiff wire collar with spool of thread attached, to holes that presumably were their home burrows. Data obtained in this manner indicated that ordinarily several or many individuals use the same burrow system. The histories of individual voles on the study area at the Reservation indicate shift of home base from time to time, usually for short distances within the area already included in the home range, but occasionally to new areas relatively remote from the original home range.

Severe fighting between adult prairie voles occurs at times. Occasionally, sharp squeaks accompanied by brisk rustling in the grass suggesting pursuit or conflict, are heard in their habitat. An unusually large adult male, long resident on a study area, suddenly lost weight and deteriorated in condition over a period of several days, then was found dead in a nest-box attached to a trap. Dissection revealed numerous punctures in the skin and flesh of the neck and back, probably made by the incisors of another vole. Extensive hemorrhage and swelling had occurred, and obviously these injuries were the cause of death.

Although it was not feasible to study the home life of the voles underground, clues were gained from those uncovered in runways and nests beneath large boards and strips of tarpaper, previously distributed for this purpose. Nests were constructed by the voles beneath several such pieces of tarpaper and runways appeared beneath all the pieces that were placed in habitat favorable to the voles. In summer, however, the high daytime temperatures beneath these shelters made them uninhabitable to the voles, and they were used mainly in spring. From February 15 to May 1, 1953, 14 voles were caught 19 times beneath five of the tarpaper strips, and many other voles that were seen beneath them escaped. Upon turning one of the strips I often discovered voles in close proximity. Sometimes two or more darted from the same nest. The disturbance of repeatedly raising the strips and exposing the voles' shelters soon caused them to desert the sites; consequently the information obtained by this means was limited.

SEXUAL BEHAVIOR

There is sexual activity in every month of the year, but its incidence varies greatly from one season to another. As has been indicated by various authors, male voles reach sexual maturity later than females. It seems that ordinarily the availability of sexually active males is not a limiting factor, however. While males that are still well below average adult size produce mature spermatozoa, and are probably capable of breeding (Jameson, 1947: 145), certain large old males may sire a disproportionately large percentage of the litters produced. Observations on males in confinement indicated that sexual activity tended to be directly proportional to the size of the testes. Occasional individuals, having much enlarged scrotal testes were more readily stimulated to sexual activity and more aggressive toward females than were those in which the testes were of more nearly typical size or abdominal or were smaller than normal. The combination of factors controlling size of testes is not well understood, but males having unusually large testes were caught most often when food supply was optimum, for instance after a period of heavy precipitation when an abundant supply of new grass provided succulent and nutritious food.

In confinement sexual activity was largely inhibited and attempts to establish a laboratory colony met with failure. Sexual activity was observed mainly in recently captured males, and their interest was aroused chiefly by females that had given birth to litters within a few hours previously. Oestrus is known to follow closely after parturition. Females found in live-traps with newborn young often were brought to the laboratory for observation. An apparent instance of hostility between rival males competing for an oestrus female was observed on September 2, 1950. The female was found in a trap with four newborn young, and since the young had not yet attached to her teats, she was temporarily returned to the trap after recording, to prevent desertion of the litter. Returning twenty minutes later I found another adult vole at this trap. It would suddenly emerge from dense grass nearby, and would move over the trap or around it, with jerky, halting movements, then would dart back under cover. The female emerged from the nest box into the trap runway, and sniffed at the other, and both pressed against the intervening wire barrier. There was gnawing on the wire by one or both. A third adult vole appeared. As it moved toward the trap, all three suddenly took alarm and darted back under cover, the female hiding in the trap nest box. In a few seconds they again appeared. The two outsiders, presumably both males, were not individually recognizable, but several times one was seen to dart at the other, chasing it away momentarily. They were seldom both in sight at once.

Males confined with post-partum females usually evinced sexual interest, following them about persistently and nuzzling their genitalia. The females, however, were often unreceptive perhaps because they were disturbed by strange surroundings and by the presence of their litters, so that they usually attempted to escape, or to rebuff the male's attention. At first the female might flee, squeaking in protest at the male's pursuit. If he still continued to follow, she would turn on him, rearing back in the characteristic threatening pose, and would lunge at him, striking him sharply or driving him back. After such rebuff, males were usually intimidated or discouraged so that they temporarily or permanently abandoned their advances, and small males were more easily rebuffed than were larger individuals. On several occasions large males having enlarged testes were not readily rebuffed by females but continued to follow them. When the female turned upon him, such a male might lunge against her, throwing her off balance, and causing her to attempt to escape, and then continuing the pursuit until it ended in copulation or in more severe fighting. Although not accepted sexually, a rebuffed male might be readily accepted as a nest-mate, huddling along with the female and perhaps other individuals of both sexes. In huddling voles, the most frequently observed type of social behavior was grooming; one individual would slide its chin or muzzle through the other's fur with a stroking movement consisting of a series of rapid forward jerks and the stroking movements might continue for periods of minutes. The recipient of the grooming usually made no evident response indicative of either pleasure or displeasure. Often it seemed to be sleeping while the grooming was performed. Individuals of both sexes performed this grooming and the recipient might be of either the same sex or the opposite sex. This grooming may have some significance as a search for ectoparasites such as fleas, or mites that often infest the voles. However, after prolonged grooming by a companion, a vole's fur was of mussed and disarranged appearance. Although the grooming that occurs between voles that are resting in nests seems to have no direct significance as sexual behavior, somewhat similar actions constitute part of the mating pattern. A sexually aroused male overtaking a receptive female, slides his chin forward along her back with jerky, stroking movements. In some observed instances this behavior continued intermittently for several minutes before actual copulation. In some other instances it was almost lacking.

CHANGES IN FEMALE GENITALIA

In female voles that are sexually quiescent, both those that have not yet attained breeding maturity, and those that have undergone regression after attainment of sexual maturity, the vaginal orifice is not evident. The canal is sealed externally by a membranous layer of epithelium. Presence of a vaginal orifice indicates that the individual is in some active stage of the breeding cyle. The appearance of the orifice varies between different females, and it changes in the same female from day to day or even from hour to hour. Presumably these changes in the vaginal orifice are cyclical and are closely correlated with oestrus, but attempts to trace them were unsuccessful largely because the normal cycle was rapidly suppressed in captive voles, which soon became sexually quiescent. Individual voles living under natural conditions were not trapped with sufficient regularity to permit tracing the details of changes in their genitalia.

In those females having the vaginal orifice most developed, the margins are turgid and slightly inflamed. The circular opening gapes 1.0 to 1.5 mm. in diameter when the tail is raised. A female may remain in this condition for two days or more. Vaginal smears at this stage often showed nucleated cells characteristic of oestrus. Subsequently the margins of the orifice become less prominent and the opening becomes smaller. The dorsal and ventral walls adhere until an opening is no longer evident unless the adjacent skin is stretched.

In pregnancy the orifice is occasionally sealed, but usually is evident. It is, however, less prominent than in oestrus, and does not gape. The margins are less turgid than in oestrus, and the opening is in the form of a transverse slit through which the purplish epithelial lining of the dorsal wall of the vagina can be seen. After parturition, placentae and bloody discharge often are in evidence in the vaginal canal. Females that have not given birth to young recently may also have bloody mucous discharge. Its significance has not been determined. In females that are undergoing sexual regression, the margins of the vaginal orifice become shrunken and pale, and the orifice becomes partly or wholly sealed.

Bodenheimer and Sulman (1946: 255) concluded from their study of *Microtus guentheri* that in this species, as in "the cat," "the rabbit," "the ferret," and a few other mammals, ovulation is induced by copulation, and that there is no regular vaginal cycle. Hoyte (1955: 412) disagreed with these conclusions for other species of *Microtus*, as he trapped individuals of *M. oeconomus* that had recently ovulated without copulation (at least no sperm were found in the genital tracts). In *M. ochrogaster* oestrus seems to be controlled largely by the food supply, at least the incidence of perforate females was found to fluctuate irregularly tending to follow the trend of rainfall, and, probably in more direct correlation, the amount of new grass present (see Table 1, and Martin, 1956: 383-384). It therefore seems unlikely that in this species ovulation is dependent on copulation.

In females that have not yet produced young the teats are minute and well concealed in the fur, so that they are difficult to find, but in lactation they become conspicuous. In early lactation the teats are typically about 1 mm. in diameter and 2.5 mm. in length. As lactation progresses, they become thickened to nearly twice the original diameter. After lactation, as inversion occurs, they shrink to scabrous low prominences, 2 mm. to 3 mm. in diameter, surrounded by bare skin. There are three pairs of mammae, one pair pectoral and the other two abdominal. As mentioned by Jameson (1947:146), the pectoral mammae show little evidence of use in lactating prairie voles. Probably they are not used at all except in females with more than the four young in a litter accommodated by the abdominal mammae. As in various other rodents, the suckling young may cling to the female's teats and may be dragged over the ground as she moves about. When the female forages near the nest, she may drag the young with her instead of leaving them, but she can detach them instantly if she so desires. On many occasions females found in live-traps had young that were several days old clinging to their teats. In some instances young that had their eyes open may have followed the female into the trap and attached afterward.

SEASONAL INCIDENCE OF BREEDING

In the region of my study the prairie vole breeds the year round, but the rate of breeding changes continually. There is no regularity in the trend of the breeding season from year to year. It is obvious that the species is responsive to environmental changes and is so well attuned that its breeding is speedily initiated or inhibited by changes to favorable or unfavorable weather. The incidence of breeding is highest when temperature is moderate and both water and foods of preferred sorts are plentiful.

Tables 1 and 2 and Fig. 1, based on 11,109 records representing each month over a four-year period, show the changing trends from month to month. The perforate condition recorded in Table 1 may represent any of several stages in oestrus or pregnancy, but is regarded as a crude index of rate of breeding, since voles in the anoestrus stage lack the vaginal orifice. Highest percentages of perforate females occurred in the months of February, March, April, May, and June, while by far the lowest percentages were recorded

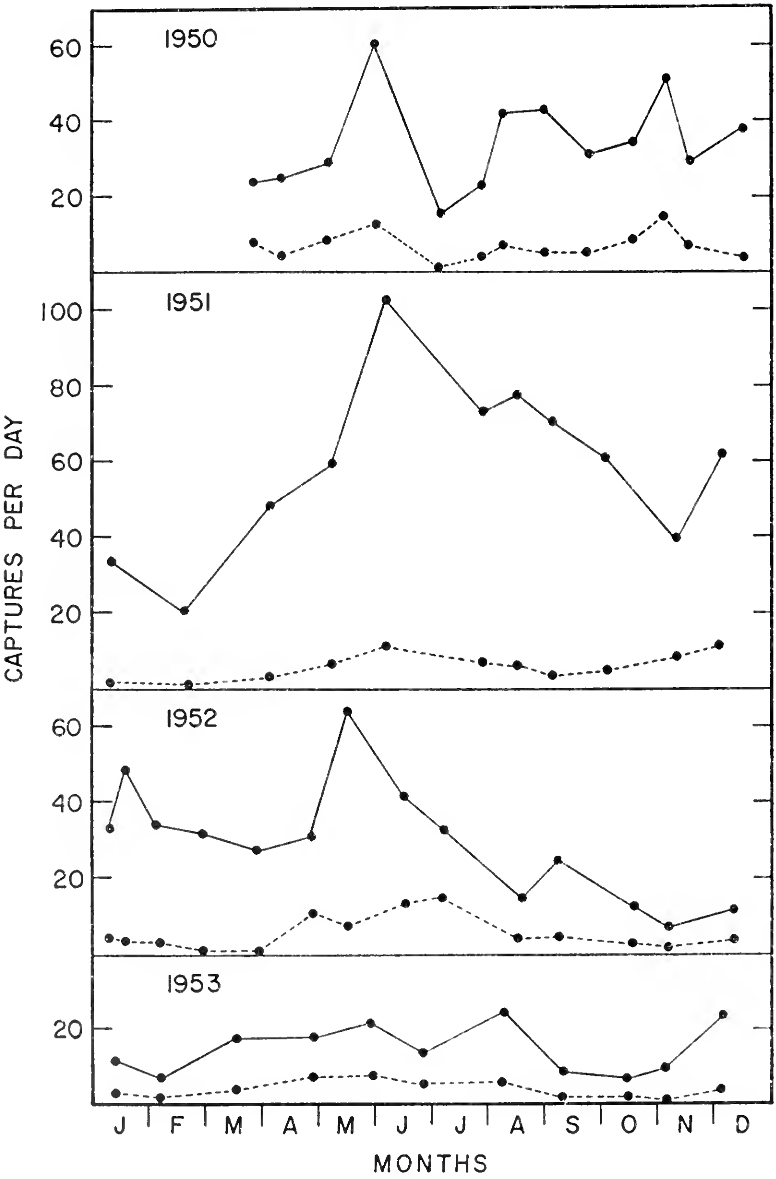

Fig. 1. Average catch per day in a three-acre field, in a grid of 100 live-traps, over a four-year period. For each year, solid line represents total and dashed line represents number of young up to 30 grams in weight. Numbers caught are roughly indicative of population density, but many variables distort this relationship. Young are never represented in the catch in their true ratio to adults, since on the average they are less vagile and less attracted to traps.

in the drought summers of 1952 and 1953. Even in mid-winter a substantial proportion of the females trapped were perforate.

Usually pregnancy can be recognized only in the last week before birth of the litter, when the female's abdomen is noticeably distended by the enlarged fetuses. Palpating to detect embryos was not attempted because of the danger of injuring them or the female. Because gestation is of approximately three weeks duration, the figures in Table 2 represent roughly perhaps one-third, or a little less, of the adult females actually pregnant. At most times of year a substantial proportion of adult females (sometimes nearly all) are pregnant. Only in the winter (including March in 1951) were samples taken in which no recognizably pregnant females were found. Incidence of pregnancy was notably high in July, August, September, and October of 1950, May, 1951, May, 1952, and April and May, 1953. A high rate of breeding was not necessarily followed by an increase in the population. A relatively low rate of breeding was adequate to maintain the population level, provided that environmental factors remained favorable. Fig. 1 shows the average catch per day (with approximately 100 live-traps) over the four-year period, 1950 through 1953. The young (including all those weighing 30 grams or less, and corresponding roughly with the part of the population less than two months old) are shown separately. It is noteworthy that through-

TABLE 1. PERCENTAGES OF ADULT FEMALES RECORDED AS PERFORATE IN THE MONTHLY SAMPLES FROM 1950 THROUGH 1953.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1950...	......	......	40.6	76.0	81.0	67.7	57.3	43.1	47.0	44.8	21.4	31.1
1951...	27.3	47.7	38.5	41.9	40.0	41.5	45.5	52.2	56.5	48.9	45.0	45.0
1952...	41.7	53.1	77.0	51.9	52.0	19.3	12.7	5.4	51.6	43.4	24.1	37.5
1953...	33.3	72.9	50.0	73.0	58.2	16.6	15.4	31.3	56.2	60.0	61.5	41.6

TABLE 2. PERCENTAGES OF ADULT FEMALES RECORDED TO BE IN LATE PREGNANCY IN THE MONTHLY SAMPLES FROM 1950 THROUGH 1953.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1950...	......	......	5.8	8.0	21.0	13.3	57.3	43.8	40.4	45.2	7.0	0
1951...	2.3	0	0	19.4	37.1	14.9	6.7	15.2	15.0	21.9	8.9	0
1952...	0	10.4	22.6	22.6	29.5	16.5	7.9	10.8	20.3	18.9	3.3	0
1953...	0	9.1	13.3	27.5	39.4	5.5	3.8	12.5	6.2	10.0	23.0	8.3

out the entire period the ratio of young to adults tended to be fairly stable—usually fluctuating between ten and thirty per cent of the total catch. Ratios of young to adults were notably high in March and May, 1950; April, June and July, 1952; and April, May and June, 1953. Ratios of young were notably low in June and December, 1950; January, February, March, and June through October, 1951; January, February, and March, 1952; and November, 1953.

In Fig. 1 the catch per day of voles, varying from month to month, reflects chiefly the changing population density. However, other factors also have important effects on the catch. For example, bait acceptance is better in the winter when natural foods, especially greens, are scarce, with the result that a higher catch can be made with the same population density. Interference with the trap line by other animals also affected the catch of voles. In warm weather the traps were checked in both morning and evening, and the catch was correspondingly greater than it was in cool weather when the traps were checked only once daily. The ratios obtained of young to adult voles cannot be accepted at face value as the true ratios in the population, either. For the first several days of each trapping period, the voles caught were mostly adults previously marked and, presumably, conditioned to the grain bait. Later, young voles not previously recorded, came to the traps in increasing numbers. The young, being at first not conditioned to the bait, and also having relatively small home ranges, would generally be less well represented in the catch than would the adults.

GESTATION

In other species of *Microtus*, so far as known, a 21-day gestation period seems to be the rule (Bailey, 1924; 528; Hamilton, 1941: 13; Hatfield, 1935: 264). *M. ochrogaster* seems to conform to this pattern, but the data obtained were meager, because breeding activity was usually inhibited in voles kept in confinement.

A female live-trapped on July 23, 1951, appeared to be in breeding condition. When trapped two days later, she had a copulatory plug, and 21 days after this she was found with a newborn litter in a trap. A female thought to have given birth to a litter between successive captures on July 20, and July 21, 1951 (on the basis of appearance of genitalia, and reduction in weight from 53 to 46 grams), appeared to have just completed parturition when she was examined on August 10. A female that gave birth to a litter in confinement on May 18, 1954, bred and was released the same day. She was recorded as pregnant in the first week of June, but on June 7 was no longer pregnant. If this pregnancy terminated normally, a gestation of 20 days or less is indicated.

Greenwald (1956: 221) suggested that in *M. californicus*, oestrus might occur in the period of lactation, because he found recently formed corpora lutea in lactating females. In the course of my field work on *M. ochrogaster*, I obtained precise or approximate dates of successive litters born at intervals of somewhat more than 21 days apart. In different females, intervals of 23, 23, 24, 26, and approximately 27 (between 26 and 28) days were recorded between successive litters. In four other females intervals between litters were known only approximately because one of two records was based on a capture in late pregnancy judged to be within two or three days of parturition. For these females, intervals of 23, 24, 24, and 26 days were recorded. From the trend of these records, it seems that females often became pregnant within a few days after birth of a litter. Pregnancy from post-partum oestrus would seem to be less frequent than pregnancies beginning a few days after birth of the previous litter, and within the period of lactation.

NUMBER OF YOUNG PER LITTER

Jameson (1947: 146) found an average of 3.4 young per litter in 58 litters of *M. ochrogaster* from northeastern Kansas, mostly from Douglas County. Martin (1956: 386) recorded a somewhat lower mean of 3.18 ± 0.24 in 65 litters on the Reservation in 1950, 1951, and 1952. For a total of 82 litters recorded from 1950 through 1956, inclusive, I obtained an average of 3.37 ± .075 young per litter. Several litters that were recorded were excluded from this computation as in each instance there was reason to suspect that they were incomplete. These included instances of females found in traps with young several days old, females that may not have completed parturition when they were released with newborn young, and those litters that might have sustained losses through cannibalism by the mother or her trap-mates.

Mean numbers of young per litter were found to vary from year to year and from month to month, as shown by the following lists: 1950, 3.0 (13 litters); 1951, 3.5 (23 litters); 1952, 3.5 (11 litters); 1953, 3.4 (5 litters); 1954, 3.4 (15 litters); 1955, 4.1 (7 litters); 1956, 3.8 (5 litters); January 2.0 (1 litter); February 3.5 (4 litters);

March 4.5 (4 litters); April 3.9 (12 litters); May 3.3 (25 litters); June 3.0 (9 litters); July 2.7 (4 litters); August 2.9 (7 litters); September 2.8 (6 litters); October 3.4 (7 litters); November 5.0 (2 litters); December 4.0 (1 litter).

These differences can be logically explained on the basis of changes in the average age of the breeding females in the population. On the average, with greater length, weight and age, females produced progressively larger litters, although individuals did not necessarily conform to this general trend. For 24 females recorded in 1954-1956 and measured within a few days of birth of their litters, average length was correlated with number of young as follows: 6 young, 163.5 mm.; 5 young, 158.0 mm.; 4 young, 157.7 mm.; 3 young, 154.6 mm.; 2 young, 160.5 mm.

For 48 other females, recorded in 1950-1953, that were not measured, but that were mostly assignable to broad age groups on the basis of their individual histories in the trapping records, the following well defined trend was demonstrated.

TABLE 3. NUMBER OF YOUNG PER LITTER CORRELATED WITH AGE OR SIZE OF FEMALE.

AGE OR SIZE GROUP OF FEMALE	Number of females in sample	Average number of young per litter
More than one year old	4	4.25
6 to 12 months old	16	3.50
Large (age indeterminate)	9	3.44
2 to 5 months old	9	2.90
Small and medium (age indeterminate)	10	2.80

It seems that the exceptionally high average numbers of young per litter in March and April result from the breeding females in those months being nearly all fully mature survivors of the previous year. In summer, when many females that are only a few weeks old become pregnant, the average litter declines to less than three young. The small average litter of 3.0 young for 1950 probably resulted from the fact that the population on the Reservation was then expanding rapidly in the newly favorable habitat created by one year's crop of vegetation after discontinuance of grazing, and had an unusually high percentage of breeding females that were not fully adult.

SIZE AT BIRTH

In four newborn young, total lengths, in mm., were 47, 45, 45, and 42. From the length-weight relationships shown in Fig. 2, it seems that a length of approximately 47 mm. is typical of newborn young of average weight. Martin (1956: 388) found a mean weight of 2.8 ± 0.36 grams in sixteen newborn prairie voles from the Reservation. For a series of 67 other newborn voles representing 27 different litters in seven different years, I found an average of 2.9 ± .05 grams. Young ranged in weight from 3.8 to 2.0 grams. Weights of the newborn voles could not be correlated with season, size, age of females, or food conditions. However, a distinct trend toward larger size in those litters that contained fewer young was evident, as shown in Table 4.

TABLE 4. WEIGHT OF NEWBORN YOUNG, CORRELATED WITH NUMBER OF YOUNG PER LITTER.

KNOWN YOUNG PER LITTER	Mean weight in grams	Number of litters in sample	Number of young in sample
2	3.1±.09	7	13
3	3.0±.17	11	28
4	2.7±.22	6	17
5	2.6±.42	3	9

EARLY GROWTH

Voles less than 100 mm. in total length were seldom captured, because those less than this size are dependent on the female, and rarely venture far enough from the nest to be caught in a trap. A further difficulty in obtaining growth records on the smallest young is that of making accurate measurements. During their first few days they partially retain the fetal posture, usually lying on one side, with the head, body and tail flexed in an arc almost completed by the tail approximating the muzzle. Straightening the animal by stretching it and holding it with sufficient firmness to obtain a measurement might have involved injury to it. Therefore, in most instances the newborn voles examined were merely weighed or an approximate measurement was estimated without stretching the young to its full length.

Newborn voles were obtained when females that were caught in live-traps produced their litters before they were found and released. In some instances, females caught while in late pregnancy were retained in the laboratory for a day or more until parturition occurred. Many of the newborn voles were marked by toe-clipping, according to the same system used for adults. Early growth was measured in some instances by keeping the female with her litter in confinement, measuring and weighing the young at intervals. In most instances, the female was released at the point of capture (presumably near her nest burrow) with the young clinging to her teats. For the young so released, the incidence of recovery was remarkably low, seeming to indicate that they were subject to decimating losses. Perhaps such losses are normal, at least on the study area where voles are live-trapped regularly. Holding of adults and partly grown young in live-traps ordinarily has no harmful effects on them, but the resultant separation of females from newly born litters may often result in death of the young either from hunger and exposure, or from attack by other voles and natural enemies.

During the first ten days the increase in length from an original 47 mm. is from three to four mm. per day. Figs. 2, 5, and 8 show length and weights of voles whose ages in days were definitely known because they were born in the laboratory, or in a live-trap after the female was caught there. Young voles marked at birth and released with the female were rarely recovered in the period of suckling, as they ordinarily remain in the nest burrow when the female ventures out to forage. Litters retained in the laboratory therefore have provided most of the records of growth in suckling young. Growth varied greatly between litters. It was not clearly correlated with size of female, size of young at birth, or number of young in litter, but probably was influenced by attentiveness of the female, her adjustment to captivity, and her productivity of milk. Within each litter there were usually persistent differences in development, but these were minor (except for those of occasional runts) compared with the differences between litters. In several litters of five young, one was usually smaller than the others at birth and therefore could not compete successfully with its litter mates, so that it never gained possession of a teat other than one of the pectoral pair, and always succumbed within a few days, after failing to gain weight as its litter mates did. The relatively few voles marked at birth and recovered after developing under natural conditions, did not deviate from the trend of those in confinement.

CARE OF YOUNG

Females in confinement were attentive to young, and, soon after parturition, licked them clean and huddled over them protectively. Ordinarily, the newborn young soon attached to a teat, and spent a large part of its time attached during its early development. Females found in live-traps with their litters of young less than a day old, often had some or all of the young clinging to their teats. Females with newborn litters, when released from live-traps, always left without attempting to retrieve any young that were unattached. Such young usually were permanently deserted, but in some instances disappeared within an hour or less, perhaps rescued by the female returning for them.

Females with newborn young were made far more aggressive than most other voles by their tendency to protect their young from possible danger. In captivity such females usually took the offensive in attacking or rebuffing any other voles confined with them. Post-partum females obviously in oestrus were prevented from being fully receptive by their hostility toward males whose presence might endanger the young. Such a female has been seen to turn on a pursuing male and attack him viciously, several times within a few minutes, before copulation occurred. In captivity, at least, such attacks would soon discourage a male so that unless he was exceptionally active sexually, mating was prevented.

Cannibalism, involving destruction of the newborn, is probably an important factor in the population dynamics of the prairie vole. Only a small percentage of the young known to have been born on an area ever survived to be live-trapped; this small percentage was indirect evidence of decimating losses in the young. Under unfavorable conditions each of several females killed and ate her own litter, but the degree of provocation varied greatly among individuals. Females that gave birth to young in live-traps occasionally ate one or more of their newborn young, as evidenced by discarded remnants. Perhaps other instances passed unnoticed because no remnants were found. That need for food or moisture as well as psychological stress often motivated such cannibalism was suggested by the fact that surviving litter mates might be accepted and cared for by a female that had already eaten one or more of her young. Although cannibalism is most likely to occur within a few hours after birth of the young, they may be killed and eaten at any stage of development. One female that had probably eaten one or more of her litter, soon after parturition, nursed the two survivors. When these were two weeks old, all were "pastured out" in a wire mesh cage in tall brome grass. When the supply of grass had become scarce (though some was still available), the female killed and partly ate both her remaining young.

One female was captured with three young attached that were several days old. The young were detached from the female's teats with great difficulty. When these young were returned to the female a few minutes later, after they had been measured, weighed and marked, she attacked them viciously, and within a few seconds had killed all of them by biting their heads. In this instance the dead young were not eaten, although they were temporarily left with the female.

Females with young have ample cause for their circumspective demeanor toward adult males, which are especially inclined to eat the newborn. A male engaged in sexual pursuit has been observed to grasp a young dangling behind the female, pull it from her teat, and pausing momentarily, nibble its head off, before continuing to follow the female. Like the genitalia of the post-partum female, the newborn young seem to have an odor that attracts and excites the male.

To a lesser degree, adult females also display marked interest in the newborn young of other individuals, which is liable to result in cannibalism. The incidence of cannibalism is affected by the condition, collectively, of the population of voles, and the availability of nutritious food and moisture. In periods of summer drought the grass becomes coarse and fibrous, and its protein content declines. Under such conditions many voles appear to be undernourished, and some are actually emaciated. Dehydration may be an important factor at times when dew is unavailable for drinking and the green vegetation remaining is exceptionally low in moisture content. Voles caught at such times and brought to the laboratory, drank avidly, and gained several grams soon after being offered water or succulence. Cannibalism by adults on newborn young in times of drought may be motivated by the acute need for moisture and nutritious food. In times of drought the birth rate is at low ebb.

Adult males have never been observed to display paternal solicitude toward young, but some individuals, kept with females and their litters, did not molest the young and were accepted by the females as members of the family group.

Other things being equal, cannibalism involving the young might be expected to be greater at times of high population density. Then, young left in the nest by a female in the course of her foraging would more often encounter adults and partly grown young, both those that lived in the same burrow system and exploring intruders from other areas.

The eyes open at an age of nine or ten days. Then the young enter upon an exploratory period, when each wanders out of the nest, emerges from the burrow, and wanders through the adjacent surface runways in frequent short forays, sometimes following the female and sometimes alone. Such forays usually cover only a few inches at first, but as the young vole grows, becomes familiar with its surroundings, and takes more plant food, its sphere of activity gradually widens, and family ties are dissolved. Voles reared to an age of three weeks in the laboratory and then released, survived just as well if the female was not released with them demonstrating that they were fully capable of shifting for themselves at this age. In confinement, however, young voles of greater age continued to suckle and remained closely associated with the female. Females in confinement evinced much uneasiness because of their inability to evade the young when the latter were old enough to walk. The young then followed the female continually and suckled whenever she stopped or even while she moved about, unless she paused to remove them from her teats, but they would not remain detached for more than a few seconds. When a young followed the female away from the nest and then attached to a teat, the female after pulling the young from her teat, would usually carry it, grasped between her incisors, back to the nest and deposit it there. On one occasion a young vole caught in a live-trap was partly plucked and eventually killed by the female on the outside trying to pull it through the wire mesh.

On several occasions, young were successfully transferred from the mother to another lactating female in confinement, which accepted them as part of her own litter. Young, up to the time of weaning, appeared not to differentiate between the mother and other adult voles. They would follow any larger individual indiscriminately, and would huddle against it or nuzzle its undersurface searching for a teat.

EARLY DEVELOPMENT OF YOUNG

The following notes are based upon many different litters, and give some idea of the sequence of events in their early development.

Newborn: The skin is pinkish gray dorsally and pink ventrally. In profile, sparse and exceedingly fine hairs less than 1 mm. in length are discernible. The vibrissae are approximately 2 mm. long. The skin is thin and partly transparent, much wrinkled, with some deeper folds, notably one between the knee and the heel. The young lie on their sides making violent convulsive respiratory movements. When not attached to the female's teats, they may make faint squeaking sounds.

One day old: Little changed in appearance or behavior except that the dorsal surface has become darker because of growth of hair.

Two days old: Covering of fine brown hair readily discernible on dorsal surface; lower incisors protruding about .5 mm. from the gum; upper incisors have barely pierced the gum.

Four days old: Pale brown hair averaging about 1 mm. in length over the dorsal surface gives the young a sleek, seallike appearance. The young have gained greatly in muscular co-ordination. Part of the time they may still lie on their sides, but they are able also to gain an upright sprawling posture. In crawling, they are unsteady and often topple over on their sides after taking a few halting steps. They make frequent jerky lateral flexions of the body, probably to search for a teat. Their eyes and ears still are sealed shut.

Five days old: Young have changed but little in appearance since the preceding day, but they have become notably more active, with movements better co-ordinated. When placed on a level surface they can crawl briskly.

Eight days old: Young are able to stand erect, with bodies held clear of the ground, and they can even run, but the gait is slow and clumsy, and the forequarters and hind quarters are poorly co-ordinated, so that the voles tend to fall on their sides. The fur averages approximately 3 mm. in length.

Nine days old: At this stage all young have their eyes open or beginning to open.

Ten days old: All young of this age have their eyes open, but not to their fullest extent, and the eyes are still slitlike in appearance. The young have become rather gopherlike in appearance and gait. They walk briskly but unsteadily, with bodies held high off the ground. When handled, they struggle vigorously, and try to bite. These young are similar in size and appearance to the smallest voles caught in live-traps apart from their mothers.

Thirteen days old: Hair on back has grown to an average length of 8 mm. (shorter on ventral surface, head, and limbs).

Seventeen days old: The young have become alert, and almost as quick in their movements as adults. They have molariform teeth, and are taking plant food. When a family group was examined, the young instantly detached from the female's teats and scattered. The hair on the back averages 10 mm. long and the vibrissae average 20 mm. long.

There is intense competition among the young of a litter, especially if the litter has more than the average number of young. In litters with more than four young, there is competition for the inguinal teats, since, in most females at least, the pectoral teats seem to have an inadequate milk supply. As a result, it is doubtful whether more than four young to a litter are ever able to survive. From the time their eyes open, the young compete actively. When litters in confinement were fed with fresh greens, there was nearly always quarrelsome squeaking and scuffling, as the young competed for food. At such times, they have been seen to chase and attack each other.

GROWTH FROM WEANING TO MATURITY

No individual vole was recaptured with sufficient regularity, from birth to maturity, to provide a complete growth curve. The curve in Fig. 7 is a composite based on all available records of voles that were recorded as making growth in length and were recaptured before they were fully grown, so that growth rates could be computed. The figure shows that growth is extremely rapid for the first three weeks, and thereafter slows gradually but steadily, until in individuals of adult size, the increment per day is much less than that in the small young.

Since rate of growth changes rapidly, with a slowing trend, only those young voles that were recaptured within a few weeks showed the approximate growth rate for any specific portion of the ontogenetic curve. Table 5 summarizes the records of 98 such young sorted into size groups representative of several stages in development. The slowing trend of growth in voles that are nearing subadult size is well shown by these records. Throughout the greater part of the growth curve no difference could be found in rate between the sexes. It is only after sexual maturity has been attained and growth has become relatively slow that males become noticeably larger than females. This tendency for continued growth in the adult males results in a much more marked disparity in size between the sexes in the oldest voles, as evident in Fig. 2.

Martin (1956: 389) stated that growth in young prairie voles was, in general, most rapid in the period April-May-June and least rapid in mid-winter. However, his data were based entirely

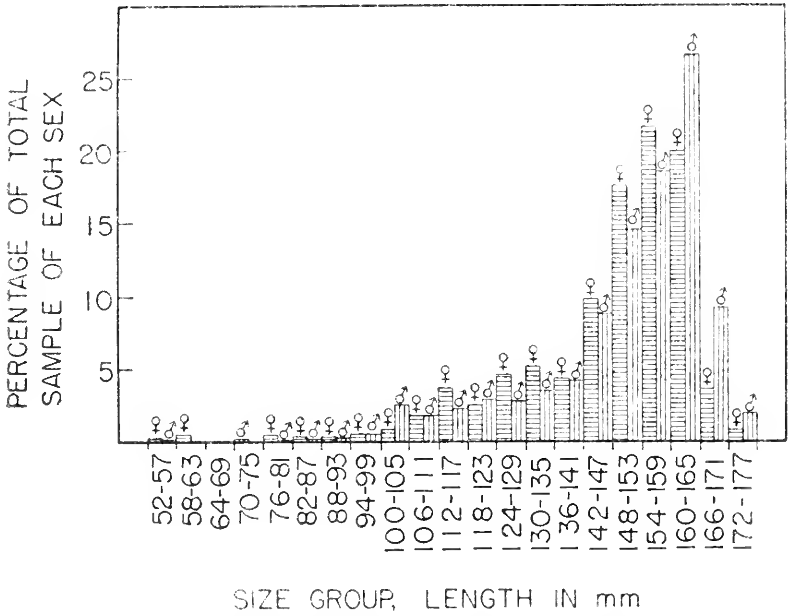

FIG. 2. Size distribution of prairie voles in a year-around sample, including all the measurements of voles taken over a three-year period. Young are not represented in their actual ratio to the total population in this sample, because they are less attracted to the bait, and range less widely than adults. The higher ratios of males than of females in the three largest size groups is well shown, as is the higher ratio of females among those voles of small adult size.

TABLE 5. AVERAGE GROWTH (IN OVER-ALL LENGTH) IN YOUNG VOLES OF SEVERAL SIZES.

Average lengths in mm. at beginning and end of growth period	Average length, in days, of growth periods	Average increment per day in mm.	Total, and number of each sex in sample
97.0 to 126.6	in 16.8	1.76	5 (1 ♂, 4 ♀ ♀)
103.3 to 127.3	in 14.9	1.61	9 (3 ♂ ♂, 6 ♀ ♀)
107.5 to 123.4	in 11.0	1.44	8 (5 ♂ ♂, 3 ♀ ♀)
114.0 to 132.3	in 17.5	1.05	6 (5 ♂ ♂, 1 ♀)
118.5 to 136.0	in 19.7	.88	6 (3 ♂ ♂, 3 ♀ ♀)
122.1 to 135.8	in 16.2	.85	15 (5 ♂ ♂, 10 ♀ ♀)
129.3 to 145.5	in 22.8	.71	4 (all ♂ ♂)
130.6 to 146.1	in 19.8	.78	12 (all ♀ ♀)
139.8 to 147.5	in 29.5	.26	10 (all ♂ ♂)
141.2 to 148.8	in 26.2	.29	23 (all ♀ ♀)

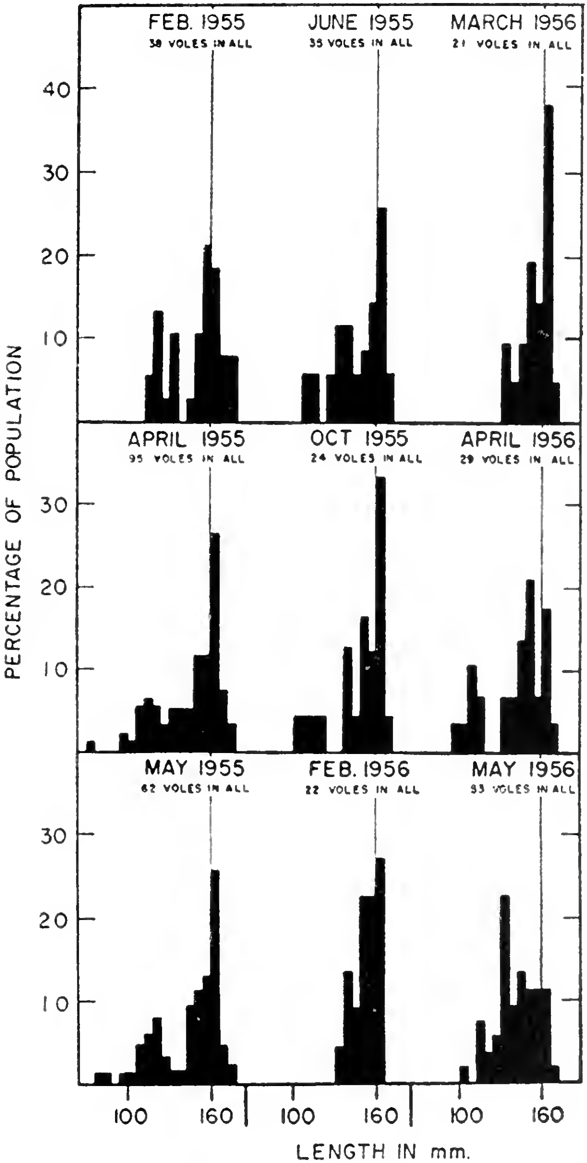

FIG. 3. Changing numbers and composition (according to size of individual) in a population of voles on an area of approximately one half an acre that was intensively sampled with live-traps over periods of months. The population as a whole and the ratio of young to adults tended to be higher in spring and summer, but with little regularity from one year to the next. Weather was far more important than season in determining the population trend. Many of the voles recorded on the half-acre area ranged more or less beyond its boundaries.

on weights. The high incidence of pregnancy in the larger young females in spring and early summer may have caused the trend. Measurements taken by me of lengths do not bear out the idea of more rapid growth in the spring and summer, but, indeed, show the opposite. In most instances, voles of comparable sizes made significantly more rapid growth in the colder half of the year (mid-October to mid-March) than in the warmer half. Dividing the young voles in eight size groups and separating each group into comparable summer and winter samples, I found more rapid average growth in the summer sample in only two instances. These

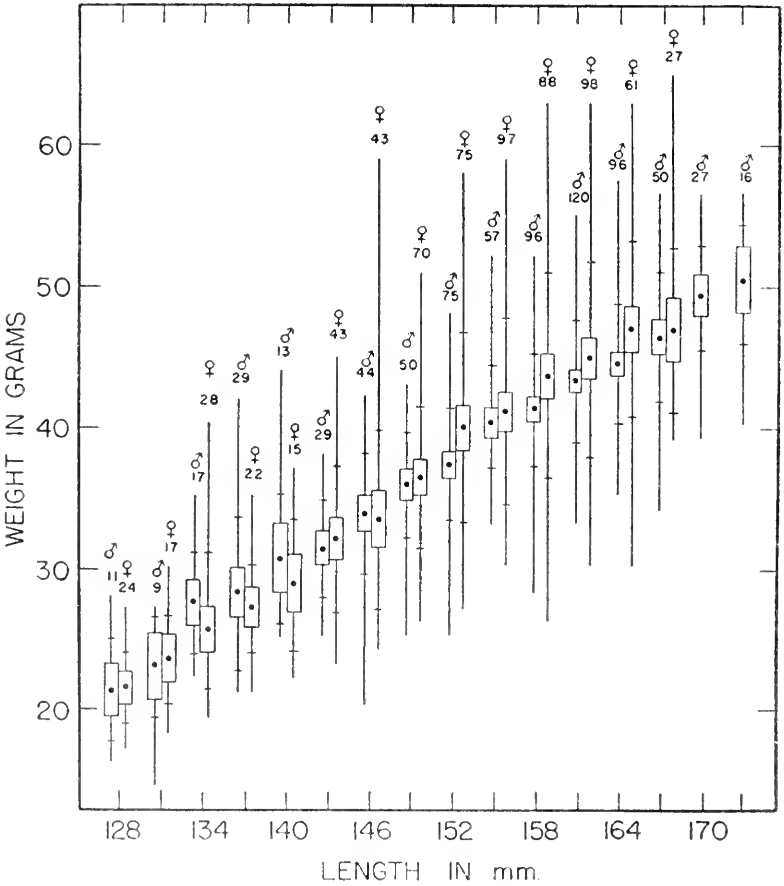

Fig. 4. Weight in free-living prairie voles in a year-around sample from juveniles to large adults (grouped in length-classes of 6 mm. range, separate for each sex). In each sample mean, standard error, standard deviation, and extremes are shown. Note that mean weight is proportional to length, that in each size class females average heavier (because of pregnancy in some) and have a much wider range of variation in weight.

deviations from the general trend probably resulted from inadequately small sizes of some samples. On the average, the growth rate in summer was 92 per cent of that in winter.

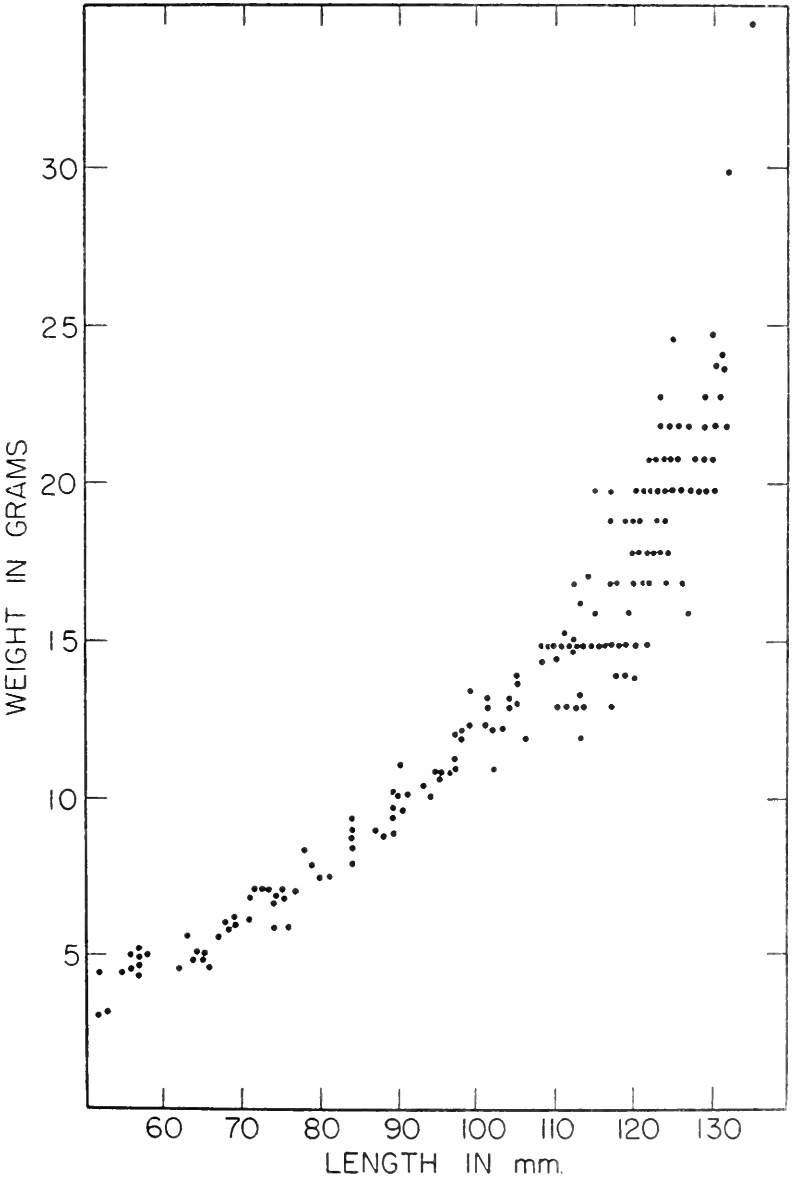

FIG. 5. Over-all length plotted against weight in young prairie voles, from newborn to the minimum size at breeding maturity. The range of variation increases as development proceeds, especially after the age of weaning is attained.

SIZE AND AGE AT SEXUAL MATURITY

Greenwald (1956: 220) found that in females of *Microtus californicus* some individuals are extremely precocious sexually, and might, at an age of as little as two weeks, produce corpora lutea and have sperm in the uterus. Greenwald mentioned one perforate female which weighed only 10 grams, but most reached a weight of at least 30 grams before their first pregnancies. The sterile cycles passed through earlier seemed to represent a "tuning-up" stage before establishment of the pituitary-gonad relationship.

Although females of *M. ochrogaster* are much less precocious in their manifestations of puberty, they may become perforate

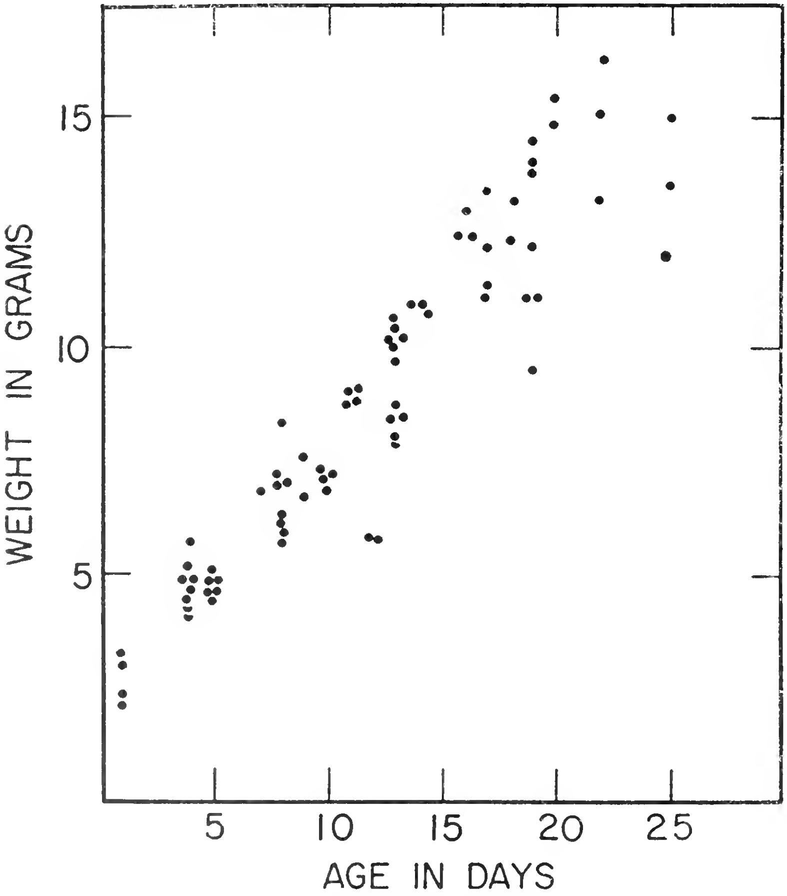

FIG. 6. Weight plotted against age in young voles, from birth up to 25 days. The range is wide at the start and increases as development proceeds.

well before impregnation can occur, and seem to pass through sterile cycles before becoming pregnant. The 18 smallest females recognized as being pregnant were of the following over-all lengths, in mm.: 149, 149, 149, 148, 148, 148, 147, 146, 145, 145, 144, 144, 143, 143, 143, 142, 135, and 134. As pregnancy is ordinarily recognized only in the last four days the females must have been impregnated from 20 to 17 days earlier—when they were in most instances 7 to 11 weeks old and 135 to 145 mm. in length. The two smallest individuals, recorded as pregnant at 135 and 134 mm., must, if they were of typical size for their age, have become pregnant at an age of approximately one month, when they were only 119 and 122 mm. in length. The smallest lactating females (some of them pregnant also) were recorded at lengths of 149, 148, 148, 147, 147, 146, 144, 144, 143, 143, and 142 mm. Occasionally females of less than 120 mm. were found to be perforate, and seemingly had begun oestral cycles. Records of a female of definitely known age, typical of many of the same size in her development, are cited below:

March 19, 1956 Born in captivity.

April 7, 1956 (19 days old) Released on study area at site of mother's capture; length 102 mm., weight 11.1 gms.

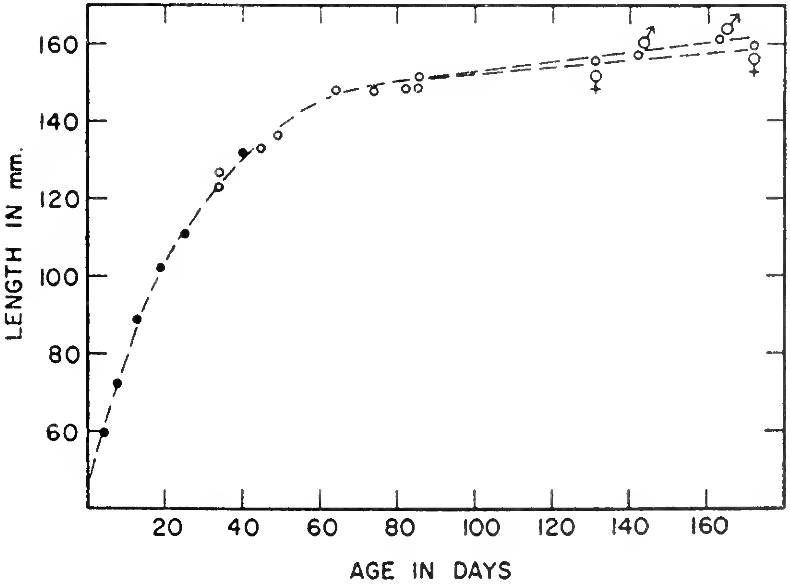

FIG. 7. Growth curve in the prairie vole; dots are based on means of series of definitely known age (born in captivity); circles are based on mean lengths of recaptured marked young whose ages were not precisely known.

April 15, 1956 (27 days old) Recaptured; perforate with a copulatory plug; length 113 mm., weight 13.4 gms.

April 27, 1956 (39 days old) Recaptured; imperforate; length 131 mm., weight 24.3 gms.

May 12, 1956 (54 days old) Recaptured; perforate and in late pregnancy; length 146 mm.

May 25, 1956 (67 days old) Recaptured; imperforate, in an advanced state of lactation; length 150 mm., weight 33 gms.

When captured on May 12, at an age of 54 days, this female appeared to be within two or three days of parturition, and hence

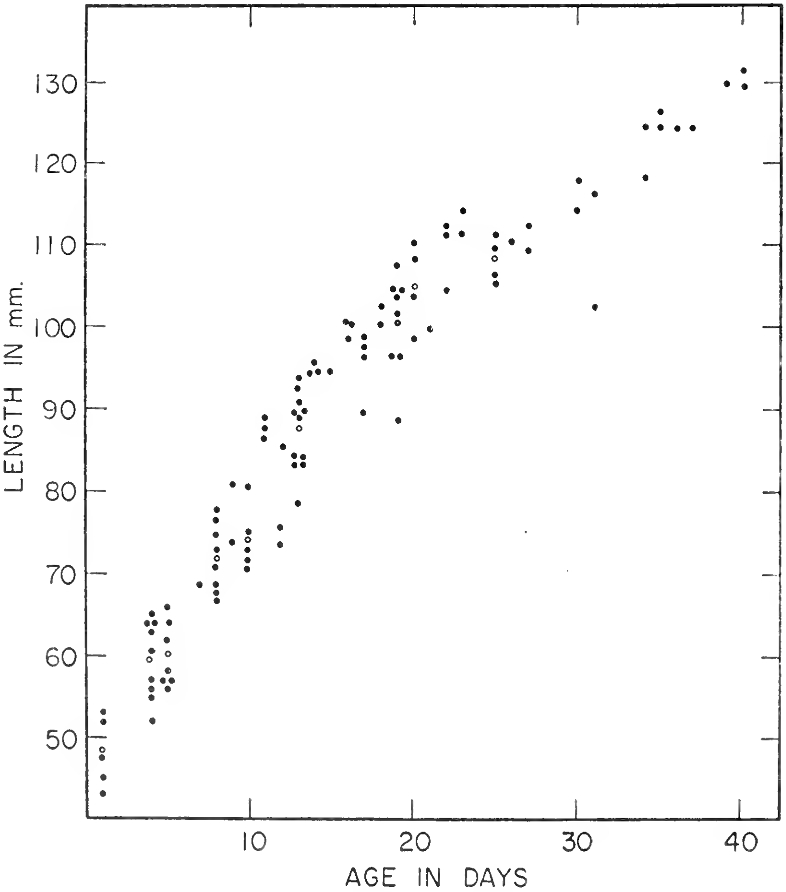

FIG. 8. Over-all length in young prairie voles of definitely known ages, up to 40 days. All were born in captivity. Some were released with the female and developed under natural conditions, but their growth rate did not differ discernibly from that of those kept in the laboratory. Dots indicate individual records; circles are means for ages at which four or more records were obtained.

must have become pregnant at an age of approximately 35 or 36 days. Pregnancy in the more precocious females probably occurs at a length of approximately 130 mm. and an age of a little less than 40 days. Such females are still growing so rapidly that by the time their litters are born, they have grown to more than 140 mm.

GROWTH IN SUBADULTS AND ADULTS

Table 6 is a summarization of 73 records of individuals that made substantial growth as adults, after they were marked and measured. These records show the slowing trend of growth with advanced age. Also, they show the wide range of individual variation in growth rate, and difference between the sexes. With advanced age, growth in females lags behind that in males to an increasing extent. Exceptionally large individuals, of either sex, are many months old, but some individuals live to be a year old or more without growing much beyond average adult size. The average growth rate of more than 1 mm. per day in young has slowed to less than .1 mm. per day, on the average, in adults exceeding 160 mm., and has slowed to less than .05 mm. per day, on the average, in those exceeding 165 mm.

TABLE 6. SIZE GROUPS (OVER-ALL LENGTH) IN RECAPTURED VOLES THAT WERE MARKED BEFORE MATURITY AND THEREFORE WERE OF APPROXIMATELY KNOWN AGES.

SIZE GROUP LENGTH IN MM.	Estimated age, in days			Number in sample
	Average	Maximum	Minimum	
171 to 175...........	♂ 435	....	....	1
	♀ 324	338	310	2
	All 361	435	310	3
166 to 170...........	♂ 304	523	179	9
	♀ 398	597	158	6
	All 346	597	158	15
161 to 165...........	♂ 227	465	104	15
	♀ 257	394	134	18
	All 243	465	104	33
156 to 160...........	♂ 188	349	107	12
	♀ 187	284	93	11
	All 188	349	93	23

SUMMARY

The prairie vole is non-territorial and somewhat social. Several or many individuals of both sexes and various sizes may use the same system of surface runways and burrows and even the same nest. In general, members of such a group are mutually tolerant. A strange vole may provoke some hostility at first, but may soon be accepted as a member of a new group. Consequently, there are frequent shifts from one home base to another. Sexual relations are probably more or less promiscuous, although a male and female may rest and travel together in a semi-permanent association. In confinement only those males having markedly enlarged scrotal testes showed interest in females that were in oestrus. Post-partum females especially were eagerly pursued by such males. Anoestrus females are imperforate, and a vaginal orifice is present only during an active oestral cycle or in pregnancy. The perforate condition therefore, is a crude index of breeding activity in the population. In adult females the ratio of those that were perforate usually fluctuated between one-fourth and three-fourths of the total. Only in severe summer drought did the numbers decline below 24 per cent. Normally, breeding continues the year around, but it is temporarily inhibited in unusually cold weather or drought. The highest incidence of pregnancy normally is in late spring and early summer. The ratio of juveniles in the population from month to month and year to year is far more stable than the actual population density.

Gestation is 21 days or a little less. The mean litter is 3.37 ± .075 young. Three is the most frequent number per litter, with four, two, and five in that order of frequency. Larger and older females have more young per litter, on the average. Average size is greater in those litters having fewer young. At birth, young are between 40 and 50 mm. in length (typically, 47 mm.), and weigh 2.9 ± .05 grams.

At an age of nine days the young have their eyes open, and they may be weaned at an age of approximately three weeks. Young suckle chiefly from the four abdominal teats. The pectoral mammae seem to be inadequately developed, with the result that in exceptionally large litters of five, six or seven young, usually no more than four survive. Until weaning the young spend much of their time attached to the female's teats. She may even drag them behind as she forages. Females that have suckling young become much less tolerant of other voles. Attacks on young, and cannibalism, are common. Adult males, especially, are liable to eat the newborn young. The acquisition of cannibalistic habits by individuals, and seasonal lack of adequately nutritious plant foods may result in the killing off of young in such numbers that the population level is held down.

In young females sterile oestral cycles often begin at about the time of weaning. Earliest pregnancies occur when females are approximately one month old, but most are several weeks older before they become pregnant. Rate of growth declines steadily from a length increment of approximately 2 mm. per day in voles less than two weeks old to an increment of approximately one-fourth mm. per day in subadults. Growth rate is highly variable among individuals at all stages, and especially in those that have attained adult size. Even adults tend to gain in length, slowly, as well as in weight, and the largest individuals are all many months old.

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19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-337. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.

2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
6. Distribution of Some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.
7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.
9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.
10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.
11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.

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12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.
13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.
14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.
15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figs. in text. June 10, 1955.

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Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 26 figs. in text. September 1, 1954.
2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.
3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.
4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.
5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.
6. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figures in text. April 2, 1956.
7. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. By Henry S. Fitch. Pp. 417-476, 10 figures in text, 6 tables. June 1, 1956.
8. Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas. By Dwight Platt. Pp. 477-498, 4 tables. June 8, 1956.
9. Ecological observations on the woodrat, Neotoma floridana. By Henry S. Fitch and Dennis G. Rainey. Pp. 499-533, 3 figures in text. June 12, 1956.
10. Eastern woodrat, Neotoma floridana: Life history and ecology. By Dennis G. Rainey. Pp. 535-646, 12 plates, 13 figures in text. August 15, 1956.

Index. Pp. 647-675.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.
4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.
5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.
7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.
8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.
9. Extensions of known ranges of Mexican bats. By Sydney Anderson, Pp. 347-351. August 15, 1956.
10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, México. By Robert J. Russell. Pp. 357-361. January 21, 1957.

More numbers will appear in volume 9.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.

More numbers will appear in volume 10.

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 10, No. 5, pp. 163-211, pls. 9-10, 1 fig. in text
March 12, 1958

Birds Found on the Arctic Slope of Northern Alaska

BY

JAMES W. BEE

UNIVERSITY OF KANSAS
LAWRENCE
1958

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*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. 1. Preliminary survey of a Paleocene faunule from the Angels Peak area, New Mexico. By Robert W. Wilson. Pp. 1-11, 1 figure in text. February 24, 1951.

2. Two new moles (Genus Scalopus) from Mexico and Texas. By Rollin H. Baker. Pp. 17-24. February 28, 1951.

3. Two new pocket gophers from Wyoming and Colorado. By E. Raymond Hall and H. Gordon Montague. Pp. 25-32. February 28, 1951.

4. Mammals obtained by Dr. Curt von Wedel from the barrier beach of Tamaulipas, Mexico. By E. Raymond Hall. Pp. 33-47, 1 figure in text. October 1, 1951.

5. Comments on the taxonomy and geographic distribution of some North American rabbits. By E. Raymond Hall and Keith R. Kelson. Pp. 49-58. October 1, 1951.

6. Two new subspecies of Thomomys bottae from New Mexico and Colorado. By Keith R. Kelson. Pp. 59-71, 1 figure in text. October 1, 1951.

7. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.

8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.

9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.

*10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202, 68 figures in text. December 15, 1951.

11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.

12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.

13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.

14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15, 1951.

15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.

16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.

17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.

18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

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UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Volume 10, No. 5, pp. 163-211, plates 9-10, 1 fig. in text
Published March 12, 1958

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1958
27-1766

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INTRODUCTION

In the summers of 1951 and 1952 some data on birds were gathered incidental to a study of the mammals of the Arctic Slope of northern Alaska (see Bee and Hall—Mammals of Northern Alaska . . ., Univ. Kansas Mus. Nat. Hist., Miscl. Publ., 8, March 10, 1956). Other students, currently preparing comprehensive accounts of the birds of northern Alaska, have urged that the information obtained in 1951 and 1952 be made available. For that reason, and because relatively little is on record concerning birds of the area visited, I have prepared the following account. The aim is to include only non-published data because the comprehensive accounts alluded to above, by others, can more appropriately include data from previously published accounts.

The area is the treeless tundra delimited by the crest of the Brooks Range to the south, the international boundary to the east and the Arctic Ocean to the north and west.

Three hundred and fifty-one birds of 44 species (Nos. 30371-30866, and 31301-31355) were collected. Twenty-nine additional species were seen. All specimens are skeletons, unless otherwise noted in the text, and are catalogued and housed at the Museum of Natural History, University of Kansas. Photographs are by the author.

The report results from a contract (Nonr-38700) between the Office of Naval Research and the Museum of Natural History of the University of Kansas. Field headquarters were at the Arctic Research Laboratory at Point Barrow, Alaska. Professor John Fields and Dr. Louis O. Quam of the Office of Naval Research, Professor Ira L. Wiggins, Scientific Director of the Arctic Research Laboratory, and Mr. M. R. Lipman of the University of Kansas Regional Office of the Office of Naval Research are four of the persons to whom I am deeply indebted. J. Knox Jones, Jr., and Edward G. Campbell, students at the University of Kansas, participated in the field work and deserve credit for a large part of the accomplishment registered in the field.

The author is greatly indebted to Professor E. Raymond Hall for assistance at many stages in the work. I am grateful to Professor Harrison B. Tordoff for numerous suggestions and for verifying the identifications of the specimens. The skeletons were identified by measurement and comparison of feet, bills, and the dried, flat skins that had been removed and labeled with the field numbers of the corresponding skeletons. Where subspecific identification was difficult because of the fashion in which the material was preserved it should be understood that the subspecific name assigned was based largely or entirely on geographic probability. This is wholly true for sight records. Robert G. Bee read the manuscript in its entirety and offered editorial comments and my wife, Annette, typed the manuscript and made numerous corrections. The names of several other individuals who rendered assistance appear at appropriate places in the following pages.

ITINERARY

Camps and collecting localities on the Arctic Slope of northern Alaska in 1951 and 1952 (Bee and Jones, July 3-September 6, 1951; Bee, September 6-11, 1951; Bee and Campbell, June 14-August 25, 1952; Bee, Campbell, and Hall, August 26-September 12, 1952) were as shown in Fig. 1.

Camps, and localities in the vicinity of each camp, are arranged geographically from north to south. The localities listed below under camps are only those which one or more of us (Bee, Campbell, Jones and Hall) visited. Travel between camps was by airplane; heavy black lines show routes followed.

POINT BARROW (1951: July 3-5, 10-12, 18-20, 27-29, Aug. 5-7, 28-30, Sept. 4-11. 1952: June 14-24, Aug. 23-27, Aug. 31-Sept. 12). Longitudes and latitudes taken from U. S. Coast and Geodetic Survey map No. 9445, 2nd edition, Point Barrow and vicinity, corrected May 21, 1951.

- Point Barrow, 156°27′25″, 71°23′11″, 3 ft. (June 20, 21, Aug. 25, 1952).
- Point Barrow, 156°30′00″, 71°22′10″, 0 ft. (Sept. 11, 1952).
- 4½ mi. SW Point Barrow, 5 ft. (Sept. 7, 8, 1951), but in the second year (June 14, 16, 1952) specimens from this same place were inadvertently labeled at "Birnirk Mounds, 156°36′02″, 71°20′40″, 8 ft.".
- NW Elson Lagoon, 156°35′45″, 71°20′27″, 0 ft. (Sept. 2, 1952).
- Point Barrow, 156°40′40″, 71°19′30″, 8 ft. (Sept. 9, 1952).
- Point Barrow, 156°35′45″, 71°19′30″, 8 ft. (Sept. 9, 1952).
- Point Barrow, 156°39′40″, 71°19′03″, 6 ft. (Sept. 3, 4, 7, 8, 1952).
- West side Salt Water Lake [Lagoon], 156°42′00″, 71°18′41″, 4 ft. (June 18, 19, 1952).
- ¹⁄₁₀ mi. W Salt Water Lake [Lagoon], 156°42′02″, 71°18′26″, 10 ft. (June 16-19, 1952).

$\frac{9}{10}$ mi. E and $\frac{8}{10}$ mi. N Barrow Village, 156°44′15″, 71°18′20″, 8 ft. (June 22, 23, 1952).

$1\frac{4}{10}$ mi. S and $\frac{6}{10}$ mi. E Barrow Village, 156°45′25″, 71°16′20″, 20 ft. (June 20, 1952).

7½ mi. S and 7 mi. W Point Barrow, 156°49′, 71°17′ (September 6, 1952).

Teshekpuk Lake (1951: July 29-Aug. 4). Shown on a map, titled "Trails and Caches 1951 Season, Naval Petroleum Reserve No. 4, . . . traced and reproduced from U. S. Geological Survey Maps, March 1945, compiled from AAF Trimetrogon photography for Aeronautical Chart Service."

NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 12 ft.

Topagaruk (1951: July 5-10). Named on map "Trails and Caches 1951 . . ." cited immediately above, but is actually seven miles due south of name shown on that map. Correct position is 155°55′, 70°34′, 10 feet; but specimens are incorrectly labeled 155°48′. . . .

Kaolak River (1951: July 12-18). River shown on map cited above under Teshekpuk Lake.

[Actual camp on] Kaolak River, 159°47′40″, 70°11′15″, 30 ft.

Kaolak (1951: July 20-27). Longitude and latitude computed from map cited above under Teshekpuk Lake.

Kaolak, 160°14′51″, 69°56′00″, 178 ft.

Gavia Lake (Aug. 19-23, 1952). Longitude and latitude computed from World Aeronautical Chart (63) Brooks Range, U. S. Coast and Geodetic Survey, 5th ed., February 2, 1949.

Gavia Lake, N White Hills, 150°00′, 69°35′, 460 ft.

Umiat (1951: Aug. 30-Sept. 4. 1952: June 24-July 3, 18-23, Aug. 16-19, 23, Sept. 12). Longitude and latitude taken from U. S. Geological Survey Topographic Map.

Bearpaw Creek, $1\frac{7}{10}$ mi. E and $1\frac{7}{10}$ mi. N Umiat, 152°04′50″, 69°23′30″, 550 ft. (June 28, 1952).

$1\frac{3}{10}$ mi. E and $1\frac{3}{10}$ mi. N Umiat, 152°05′30″, 69°23′12″, 350 ft. (June 26, 27, 1952).

$\frac{9}{10}$ mi. W and $\frac{9}{10}$ mi. N Umiat, 152°10′58″, 69°22′53″, 380 ft. (June 29, 30, July 1, 1952).

1½ mi. W and ¾ mi. N Umiat, 152°08′10″, 69°22′18″, 370 ft. (Aug. 30, Sept. 4, 1951).

Umiat, 152°08′, 69°22′, 337 ft. (Aug. 19, 1952).

Umiat, 152°09′30″, 69°22′08″, 352 ft. (June 24, 26, July 21, 22, 1952).

As shown on fig. 1 a reconnaissance flight was made from Umiat to Sadlerochit River and return (July 22, 1952).

Lake Schrader-Lake Peters (July 23-Aug. 16, 1952). Longitudes and latitudes taken from map entitled "Preliminary Copy," U. S. Petroleum Reserve No. 4, U. S. Geological Survey, March 1948, scale 1-6900.

Spawning Creek, W side Lake Schrader, 145°11′40″, 69°25′08″, 2908 ft.

SW Lake Schrader, 145°11′30″, 69°24′32″, 2925 ft. (July 27, 28, 1952).

Lake Schrader, 145°09′50″, 69°24′28″, 2900 ft. (July 23, 24-30, 1952).

East side Lake Schrader-Lake Peters Channel, 145°09′30″, 69°24′15″, 2905 ft. (July 29, 30, 1952).

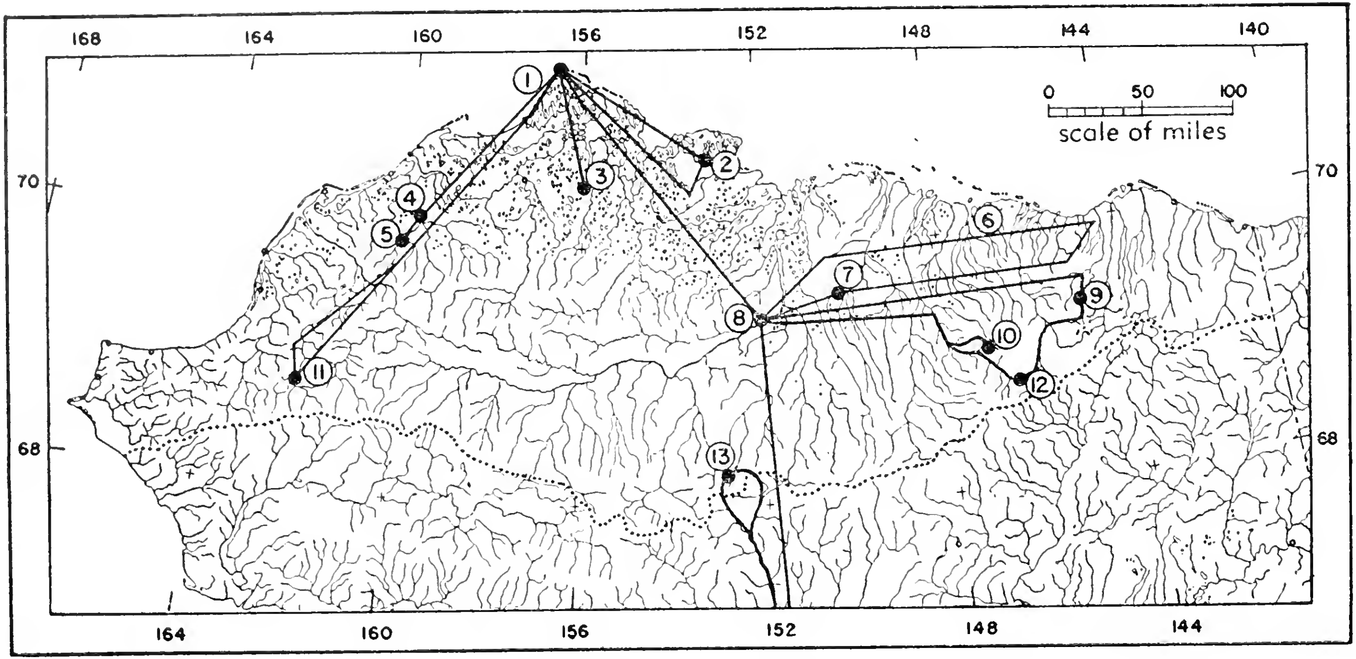

FIG. 1. Routes of travel and base camps of field party in 1951 and 1952.

1. Point Barrow
2. Teshekpuk Lake
3. Topagaruk
4. Kaolak River
5. Kaolak
6. Reconnaissance flight
7. Gavia Lake
8. Umiat
9. Lake Schrader-Lake Peters
10. Wahoo Lake
11. Driftwood
12. Porcupine Lake
13. Chandler Lake

Mouth Chamberlin Canyon, S end Lake Peters, 145°08′34″, 69°20′58″, 3690 ft. (Aug. 4, 5, 1952).

SE end Lake Peters, 145°09′26″, 69°20′56″, 2950 ft., Romanzof Mountains (Aug. 1-9, 14, 1952).

Mount Mary, S end Lake Peters, 145°10′05″, 69°20′35″, 3012 ft. (The mountain between Carnivore River on the east, Whistler Creek on the west, mouth of Whistler Creek on the north, and the crest of the Brooks Range on the south.) (Aug. 13-16, 1952.)

Mount Mary, S end Lake Peters, 145°10′02″, 69°20′30″, 2920 ft. (July 30-Aug. 11, 1952).

S end Lake Peters, 145°09′50″, 69°20′15″, 2906 ft. (Aug. 15, 1952).

Weasel Point, S end Lake Peters, 145°09′30″, 69°20′15″, 2920 ft. (Aug. 9-11, 1952).

Carnivore Lakes (Carnivore is the name of the three lakes at elevations of 3260, 3385 and 3400 ft. between 69°18′ and 69°17′ on Carnivore River, which flows from James Robert Lake to Lake Peters). (Aug. 8, 1952.)

James Robert Glacier, 145°09′, 69°16′, approximately 3700 ft. (Aug. 8, 1952).

WAHOO LAKE (July 3-11, 1952). Longitude and latitude taken from map entitled "Preliminary Copy," Naval Petroleum Reserve No. 4, U. S. Geological Survey (of same series as map used at Porcupine Lake, see below).

Wahoo Lake, 146°58′, 69°08′, 2350 ft.

DRIFTWOOD (Aug. 27-31, 1952). Longitude and latitude computed from map cited above under Teshekpuk Lake.

2 mi. W Utukok River, 161°15′30″, 68°54′50″, 1275 ft. (Aug. 30, 1952).

Driftwood, Utukok River, 161°12′10″, 68°53′47″, 1200 ft. (Aug. 27-31, 1952).

PORCUPINE LAKE (July 11-18, 1952). Longitude and latitude computed from map titled "Preliminary Copy," Naval Petroleum Reserve No. 4, compiled by U. S. Geological Survey, May, 1949, Alaska, K6, scale 1:4800.

Porcupine Lake, 146°29′50″, 68°51′57″, 3140 ft. (July 12-16, 18, 1952).

Mount Annette, 146°28′51″, 68°50′38″, approximately 5700 ft. (Mount Annette is in the Annette Range south of Porcupine Lake between the Canning River and the Ivashak River.) (July 17, 1952.)

CHANDLER LAKE (Aug. 9-25, 1951). Longitude and latitude taken from World Aeronautical Chart (63) Brooks Range, U. S. Coast and Geodetic Survey, 5th ed., February 2, 1949.

Chandler Lake, 152°45′, 68°12′, 2900 ft.

ACCOUNTS OF SPECIES

Gavia adamsii (Gray): Yellow-billed loon.—Specimens, 3: Kaolak (Kuk) River, 159°47′40″, 70°11′15″, 30 ft., No. 30571, ad. female, July 18, 1951; Wahoo Lake, 146°58′, 69°08′, 2350 ft. (a breeding pair), No. 31301, ad. male and No. 31302, ad. female, July 9, 1952.

Upon our arrival at Wahoo Lake (July 3, 1952), two yellow-billed loons were swimming, side by side, on the east end of the lake. On July 8, the pair were seen swimming close together 400 feet distant from the nest. It was located on July 4 and held two fresh eggs. Three days later at 3:00 A.M. one of the pair called directly in front of our camp, which was approximately 4000 feet from the nest at the other end of the lake. The call was the first uttered in the area since our arrival. Except for the two instances noted above, only a single loon was seen at any one time almost certainly because the other was sitting on the eggs. At 3:00 P. M. on July 9, by means of a boat, we visited the nesting area; the male was incubating and the female was absent from the area. As we approached to within 30 feet of the nest, the male, conspicuous as it sat upon the nest with neck held low and extended, became nervous. When we were 25 feet away the bird plunged into the lake. His feet and wings beat the water, increasing his speed; he flew to our right approximately 30 feet from the nest and was shot. The nest and eggs were photographed and we left the area. At 5:30 P. M., the female was swimming on the lake in the general area of the nest. In an effort to obtain the bird we pursued her down the middle of the lake, approximately 1000 feet from her nest and in the direction from which we came. Turning shoreward she dived and resurfaced approximately 300 feet in the opposite direction from which she was being pursued. Two additional dives brought her to the vicinity of the nest. No cry was uttered by either of the birds during our pursuit.

Although the female had been incubating two nearly fresh eggs, her ovary, 35 mm long and 19 mm in diameter, contained ova of various sizes up to six mm in diameter. The female measured 850 mm in total length and weighed 4536 grams; the male was 900 mm in total length and weighed 6804 grams.

The nest, approximately 60 cm in diameter, of sedges, grasses and an assortment of plant debris, was on a mound of soil 23 cm above, and 40 cm from, the open water. The cup of the nest measured 37 mm in depth. The site of the nest (southeast corner of the lake) was near the area supporting the most lake trout (*Cristivomer namaycush*). Between open water of the lake and the shore, 20 feet of sedges and grasses deterred wolves (*Canis lupus*), red foxes (*Vulpes fulva*), and caribou (*Rangifer arcticus*) from molesting the nest; tracks of these mammals were numerous on contiguous shore areas.

The early run-off entering the lake created a variable water level (the overflow decreased 60 per cent in the period July 2 to July 11). The loons lay their eggs when the lake's level is fairly well stabilized. The cotton-grass (*Eriophorum*) at the latter date was developing white flowers and the sedges, growing in dense stands, were showing springtime green.

The force with which the excrement of the loon is expelled while standing on land, accounts for long white lines upwards of one meter in length. These lines of dried excrement, reaching as far as one and one-tenth meters landward, were noted at several places along the shore.

At Topagaruk on July 9, 1951, a single yellow-billed loon was observed. At Kaolak River (July 12-18, 1951) the yellow-billed loon was occasionally heard at night and, at times in the day. On July 18, an Eskimo, Atanak, accompanied by two companions from Wainwright, shot two loons of this species approximately two miles down the Kaolak River from our camp. They had planned to prepare the birds for their evening meal. With the exception of twelve pebbles averaging 3.5 mm in diameter in the one, the stomachs of the loons were empty. The female was given to us by the Eskimos. It measured 870 mm in total length, 1600 mm in wing spread, and 5897 grams in weight. The ovaries contained many ova, the largest eight mm in diameter. Many of the individual ova were black.

At Porcupine Lake a yellow-billed loon was seen every day (July 13-18, 1952) but was not heard until 8:00 P. M. on July 17; its call was the first since our arrival on July 13. Thereafter its long drawn-out wail or raucous, hilarious call was uttered at intervals in the evening and well toward midnight.

A yellow-billed loon was on the south end of Lake Peters on August 4, 1952. At 9:00 A. M. it caught a small fish at the mouth of Carnivore River. The loon flew north approximately five miles to Lake Schrader where it was known to have young.

Of the three species of loons observed on the Arctic Slope, the yellow-billed loon is the least numerous. Owing to its large size this loon is more often taken than either of the others. Eskimos consider its dark, fine grained flesh a delicacy. On the more isolated areas of the Arctic Slope the yellow-billed loon remains common; elsewhere it needs protection.

Additional specimens, especially from the contact zone between the areas of geographical distribution of *Gavia immer* and *Gavia adamsii*, are needed in order to decide on the subspecific *versus* specific status of these two kinds of loons.

Gavia arctica pacifica (Lawrence): Arctic loon.—Specimens, 2: Barrier Lake, NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., No. 30570, ad. female, July 29, 1951; Topagaruk River, 155°48′, 70°34′, 10 ft., No. 30572, ad. female, July 7, 1951.

On July 3, 1952, between Umiat and Ivashak River, pairs of Arctic loons were on only small and medium sized lakes; on this date they mostly were free of ice whereas large lakes were ice covered and thus unavailable to this species of loon. The use of small and medium sized lakes by this loon may result from the described unavailability of large lakes at nesting time. The tundra, at this time, when nesting has begun, is free of snow except for cornices and deposits in deep gullies. Willows and alders at Umiat on July 3 were without foliage, whereas these plants farther east were in leaf. On July 4, 1951, at two-tenths of a mile south of the Arctic Research Laboratory, a single bird flew over the tundra and onto the Arctic Ocean beyond. It called regularly as it passed overhead. At Topagaruk (July 5, 1951) the pairs of Arctic loons were nesting on the vegetated edges of lakes of medium size. This species of loon constituted less than one per cent of the avian population of the area. A nest of this loon on a promontory between two lakes and within 30 centimeters of deep water was damp, shallow, slightly depressed and held eggs exposed to view. On July 7, the female was killed as she left the nest. The wind blowing offshore drifted her toward the center of the lake. Later, as she reached a point near the opposite side, the male alighted near the dead female and indulged in its courtship display of raising and lowering its head and neck. Swimming around the mate several times he continued to solicit attention from the lifeless form. An hour later we examined the off-shore and found the dead female among the sedges. By this time the male had abandoned its mate and was observed feeding in an adjacent lake. Arctic loons on several adjacent lakes could be heard. The male that had been deprived of its mate, did not respond.

The female weighed 1200 grams. The largest ovum was eight mm in diameter; others were smaller and the smallest were in clusters. On leaving the nest we placed mosses and grasses over it to protect the single egg from the parasitic jaegers. We wished to learn whether the male returned and incubated the egg. On our approach on July 8 he was on the nest but left and swam approximately 200 feet under water before surfacing. On the afternoon of the same day the single egg was cold and unattended. The male was swimming on a nearby lake some 300 yards distant. Two pairs of the Arctic loon were observed swimming on adjacent lakes. On July 9, the male was again incubating the egg.

The Arctic loon calls frequently when flying overhead. The Eskimos were adept at imitating the loon's call and were successful in having the birds respond.

At Kaolak River (July 12-18, 1951), pairs of the Arctic loon used the course of the stream as a flight lane.

On an airflight from east to west between the mouth of the Canning River Canyon and Umiat (July 18, 1952) I noted an increase in the numbers of this loon, especially over the lakes near the Colville River.

Seven pairs and two singles of this species were observed between the mouth of the Avalik River and a point 23.3 miles from the Arctic Ocean when I flew directly from Koalak to Point Barrow. In the above 33 miles of coastal plain, the greatest interval between loons was 9.7 miles, the shortest 1.9 miles, the average 5.9 miles. The last 23.3 miles before reaching the Arctic Ocean, produced no records of the loon. On a lake near the Arctic Ocean, 3.8 miles southwest from Barrow Village, a single pair was observed.

Upon our arrival at Barrier Lake, northeast of Teshekpuk Lake (July 29, 1951), there were two adult and two young Arctic loons at the south end of the lake at a point approximately 300 feet from where we camped. During our stay at the lake, the loons nearly all of the time remained on approximately 1½ acres of water in spite of being disturbed and having their territory periodically invaded by us. Adjacent to the area of the lake used by this family of loons were three small lakes connected by wide channels to Barrier Lake. Other small lakes to the east were connected by smaller channels. The loons preferred to feed in the lakes having larger connecting channels.

In the evening of the first day of observation, the female together with her two young was on land. The male was swimming approximately 200 feet out on the lake. The female was shot as she was flushed from the bank. The largest ovum was four mm in diameter. On the morning of the second day (15 hours after the female was shot) the male was observed tending the young; one young was by his side and the other had wandered to a point 40 feet away. A parasitic jaeger came and hovered above the straying young loon and then dived vertically to seize it. The male loon was too far away to reach its young before the jaeger departed. As the jaeger was leaving the area, three other parasitic jaegers pursued the first in an attempt to wrest from its beak the young loon. The contest for possession of the young loon continued as far as the eye could follow the contestants.

On August 2, at 3:35 P. M. the surviving members of this loon family—the male and the one young—rested on the water of the lake, approximately 200 feet from shore. The adult dozed with its head tucked under its wing—head end oriented into the wind except for occasional complete turns. These were made without visible change of posture. The young one alternated by swimming around its parent and resting at which time it tucked its head under its wing. Toward evening, the male was shot. A survey of the area the following morning disclosed the absence of the young loon, not to be seen again during our stay. It was noted that during our sojourn of seven days, when the male was left with the orphaned young, the parent would fly to Teshekpuk Lake some 1½ miles to the south to procure food. The young loon when left alone would dive under water when approached.

On August 4, a pomarine jaeger pursued the male loon as it was returning from fishing on Teshekpuk Lake. When the birds first were seen, the jaeger was approximately 200 feet behind the loon, but in a distance of approximately 300 feet the jaeger overtook the loon which had reached the shore of Barrier Lake. When the jaeger was ready to strike in order to make the loon drop the fish it was carrying, the loon dropped over the erosional cliff and splashed into the water. After 30 seconds of hovering over the submerged loon, which remained under water for one minute, the jaeger departed to the west. The loon came to the surface holding the fish tightly crosswise in its beak.

Numerous calls of the Arctic loon were heard on the Barrier Lake area. When a person enters the territory of a family of loons, the male makes a sound similar to a courting tomcat. The female responds with a like sound and in addition concludes her call with a high pitched note. When mildly disturbed, low gutteral notes are uttered by both sexes, and are continued as a person penetrates farther into the territory of the loons, especially when young are present. In addition to the above-mentioned calls, loons have a ravenlike call, one resembling the cackling of a domestic fowl, and another resembling the bleating of a lamb.

The male concerns himself less than does the female with the safety of the family; nevertheless, attempts were noted in which the male endeavored to decoy the intruder and allow the female and young to retreat from the area. The loons react to caribou, if these animals approach too closely to the shore line adjacent to the territory of the loons.

On July 30, 1951, pairs of loons were flying over the tundra between Barrier Lake and Teshekpuk Lake.

On an airflight from Teshekpuk Lake to Point Barrow (Aug. 4, 1951) I saw Arctic loons as follows: 63 miles from Point Barrow, one; 25 miles from Point Barrow, two; 10 miles from Point Barrow, four.

At Chandler Lake (Aug. 12, 1951), a single Arctic loon was frequently heard at the southeast end near the mouth of the Chandler River. In the evening of August 13, the wind changed from the normal southern wind to a cold wind from the north. Thereafter no Arctic loon was detected at the mouth of the river until August 22 when a bird there called at three intervals in the day. Presumably the change in direction of wind caused the fish and the loon to leave the south end of the lake. Arctic loons in other parts of the lake were heard every day from August 8 to August 25 inclusive.

On August 19, 1952, when we flew from Umiat to Gavia Lake, the loons seemed to be more restless and more easily disturbed than on our earlier flights. Wariness probably increases as the season advances.

On August 20, 1952, through August 23, 1952, six pairs of Arctic loons and 10 old squaw ducks were on Gavia Lake (named after the Arctic loon, genus *Gavia*). These were the only large birds on the lake on these dates. The loons dove as they sensed danger, emitting, before the dive, a single doglike yelp.

On September 2, 1952, at ½ mile northeast of Barrow Village, we passed an Arctic loon on the beach six feet from the waters of the Arctic Ocean. On the return trip, two hours later, the loon was again seen in the same area, now preening its feathers. As we approached it walked to the water and began to swim through the breakers of the ocean. Snow was falling, telling of the approach of the migratory season for this species.

Gavia stellata (Pontoppidan): Red-throated loon. — Specimens, 4: NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., No. 30576, ad. male and No. 30577, ad. female, July 29, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., No. 30574, ad. male, July 18, 1951 and No. 30575, ad. female, July 14, 1951.

At the west side of Salt Water Lagoon (June 17,1952) we observed a single red-throated loon feeding in the lake. At Point Barrow (June 21, 1952) 15 birds in one loose flock flew east along the shore of the Arctic Ocean.

At Kaolak River (July 13, 1951) three pairs of red-throated loons nested among high sedges along the edges of small lakes (some as small as 100 x 40 feet). Of the three species of loons on the Arctic Slope, this one chooses the smallest bodies of water for nesting. Each of two nests held two eggs approximately ½ incubated. One nest and that of an Arctic tern were approximately 30 feet apart on an island in the center of the lake. The loons arrived and departed from the lake without molestation by the terns, but whenever we approached the lake a tern would fly 300 feet out on the lake to meet us. On July 14, the female loon was shot. The largest ovum was 8 mm in diameter. On July 16, we again visited the above mentioned nest. The male was incubating and left unnoticed. While we were inspecting the nest the loon reappeared only six feet away and uttered one guttural note seemingly of surprise. The loon hurriedly swam away keeping its head turned toward us and when at a distance of 25 feet, dove again. Fifteen minutes after we left the nest the bird could still be seen swimming about in the lake. On July 18 the male was shot. It weighed 2268 grams and its testes were 10 mm long. The eggs, measuring 73 x 42 and 69 x 43 mm, of this pair of loons held embryos having natal down. Although the loon usually approached the nest from the direction of open water, several trails led to the nest among sedges. One call by these birds resembled that of a wolf and was generally given between 11:00 P. M. and 2:00 A. M. Other calls were froglike, humanlike and birdlike in quality.

On a small lake between Barrier Lake and Teshekpuk Lake (July 29, 1951) a male and female attracted our attention by uttering guttural notes and occasionally a sound resembling the meowing of a cat. This lake was approximately 200 feet long and 40 feet wide and was bordered by exceptionally high sedges. Several points of sedges projected into the lake from its edge. When the loons were approached they dove under water with a splash suggesting the sound made by a beaver as it strikes its tail against the water before submerging. A loud high-pitched shrieklike call was given just before diving. They remained under water for about 20 seconds, came to the surface, and repeated the behavior. These birds were capable of leaving the lake but remained in close proximity to their young that were hiding in the grasses and sedges along the side of the lake. Both adult birds were collected. A broken egg was on one of the points of vegetation that projected into the lake. This lake was approximately 600 feet from feeding grounds at Teshekpuk Lake where small fish three-fourths of an inch in length were numerous (30 per square foot) along the edge of the lake. Other red-throated loons were noted on July 29 through August 4.

At Chandler Lake (Aug. 15, 1951), two red-throated loons frequently fed in a small meandering creek at the south end of the lake.

Olor columbianus (Ord): Whistling swan.—On July 16, 1951, a boat with three Eskimos neared a point of land approximately ⅓ mile north of our camp on the Kaolak (Kuk) River. At 200 feet from the point, two adult whistling swans and three cygnets left the edge of the river. The female pretended to have a crippled wing and flapped upstream on the surface of the water for 100 feet and then continued at normal cruising speed. The male left the area but returned in a few minutes and joined the female as she endeavored to lure the hunters up the river. The Eskimos inspected the shore where the swans had been resting and then returned to their boat and continued up the river in the wake of the female swan which was then 200 yards upstream. As the boat approached the female, she fluttered out of their way and the boat passed at approximately 30 feet. The Eskimos did not attempt to shoot at the male, the female, or the three cygnets. The following day we inspected the area from which the swans had been flushed. Four molted primary feathers of the adults were found. Twenty feet from the edge of the river was an old nest which had been occupied the previous year. This nest was in willows and grasses one foot high. At our camp (July 12), numerous foot prints measuring 160 mm in length and 142 mm in width of the swan were noted on the north side of a sand bar in the river.

Atanak and his companions from Wainwright told us that other whistling swans were observed (July 16-17, 1951) from our camp on the Kaolak River to a point seven miles up the Kaolak River from the junction of the Avalik and Ketik rivers. In the previous month (June), these same Eskimos had observed 12 pairs of swans between Wainwright and our camp.

Branta canadensis minima Ridgway: Canada goose.—On July 8 and 9, 1951, four geese fed on a large lake at Topagaruk and when disturbed, flew from the lake in groups of two or four, never as single individuals. Upon returning to the lake they reformed in a group of four. Drilling for oil was underway there but geese, ducks and smaller water birds 300 or more feet away from the well were relatively unmolested and present in normal numbers. Men at the well told us that birds were not so plentiful in 1951 as in the previous year and that it was the latter part of May, this year being earlier than last year, when waterfowl and shore-birds arrived on the tundra. In late May 50 per cent or more of the ground is covered with snow and the lakes are frozen. Creeks and rivers are used until lakes open up. This is a time of loud clamor and nuptial performances when geese and brant call all night. The noise and much of the activity ceases at nesting time. In the cool weather of autumn (September 1), lakes freeze and the birds leave the tundra and congregate along the shores of the Arctic Ocean preparatory to flock formation and migration. Geese and ducks tarry but the shore-birds leave suddenly. The fall migrations at Point Barrow begin in the middle of August.

Branta nigricans (Lawrence): Black brant.—On June 19, 1951, two black brant flew east over the tundra at Salt Water Lagoon and continued in that direction as far as we could follow the birds with binoculars. On August 25, 1952, between Birnirk and Point Barrow, we flushed a flock of 60 brant seven times; they were loathe to leave the peninsula. On the following day, 58 brant were seen in the same area.

Anser albifrons frontalis Baird: White-fronted goose.—Specimen, 1: 9/10 mi. W and 9/10 mi. N Umiat, 152°10′58″, 69°22′53″, 380 ft., No. 31303, ad. female, July 1, 1952.

As late as June 24, 1952, white-fronted geese were in flock formation at Umiat. Eight days later (July 1), 9/10 mile west and 9/10 mile north of Umiat, a nest held six incubated eggs; the embyros showed natal down. The nest was in a depression of moss (not excavated) on a mound 45 cm above water level among polygons. The concavity of the nest was 320 mm in diameter and was lined with an 80 mm thickness of sticks, pieces of moss, stems of grass and miscellaneous material. The cup, 160 mm wide and 80 mm deep, was lined with down feathers from the bird. The nest and brooding bird blended with the vegetation of *Vaccinium*, *Arctagrostis*, mosses and lichens. When the observer was 25 feet distant the female left the nest. She measured 685 mm in total length and weighed 2268 grams. The largest ovum was three mm in diameter.

On August 30 and 31, 1951, 16 white-fronted geese were feeding on the tundra along Seabee Creek. They called frequently at night.

When we flew from Point Barrow to Kaolak (July 20, 1951), approximately 100 miles southwest of Point Barrow, 12 white-fronted geese were in one group, and on a return trip (July 27) along the same route we noted several small groups.

Upon our arrival at Barrier Lake, northwest of Teshekpuk Lake on July 29, 1951, 12 white-fronted geese were resting at the south end of the lake. They had consistently used this shore, as well as the entire east shore line as evidenced there by fecal deposits. In the seven days that we camped at this lake the geese remained in the area but never returned to their original resting grounds. In the mud and silt of a lagoon on the west side of the lake, numerous tracks of these geese were associated with tracks of caribou, Arctic fox, wolf and small shore-birds. On August 1, thirty-five white-fronted geese left the north end of the lake and flew west approximately one mile where they remained feeding and calling until midnight. On the morning of August 3, two geese flew south over our camp to Teshekpuk Lake and at 8:45 P. M., 15 flew to the west.

Chen hyperborea hyperborea (Pallas): Snow goose.—Atanak, an Eskimo, told us that snow geese were common along the coast at Wainwright in the early spring of 1951. On the date of interrogation (July 18, 1951) he reported that none was in the area.

Anas acuta Linnaeus: Pintail.—Specimens, 2: 2 mi. W Utukok River, 161°15′30″, 68°54′50″, 1275 ft., No. 31304 and 31305, ad. females, Aug. 30, 31, 1952.

At Kaolak River (July 15, 1951), the primary feathers of a female in breeding plumage were being replaced by new feathers then 25 millimeters long. She was unable to fly and had secluded herself in the sedges and grasses along the edge of a lake. On July 18, a male flew over this lake. These were the only two pintails observed in this area.

At Kaolak (July 21-27, 1951), within one mile of our camp there were four females with young in groups of 4, 5, and 6. The young birds of the group of five were 75 mm in length. On June 17, 1952, several pintails were feeding in the Salt Water Lagoon at Point Barrow.

The largest of two adult females collected on August 30 and 31, 1952, two miles west of Driftwood, was 536 mm in total length and weighed 729 grams.

On August 25, 1951, three pintails fed in a small creek at the southwest corner of Chandler Lake. They were the first observed in the area where we began camping on August 9.

Anas carolinensis Gmelin: Green-winged teal.—On September 4, 1951, one green-winged teal was on a small lake approximately 1¼ miles northwest of Umiat.

Aythya marila nearctica Stejneger: Greater scaup.—On July 8, 1952, approximately ½ mile southwest of the east end of Wahoo Lake, a nest of seven eggs of this species was located on the edge of a small lake. Three males swam together in the lake.

Clangula hyemalis (Linnaeus): Old squaw.—Specimens, 5; Barrier Lake, NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., No. 35080, ad. female and 30581, ad. female, July 30, 1951; Topagaruk River, 155°48′, 70°34′, 10 ft., No. 30582, ad. female, July 7, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., No. 50579, ad. female, July 14, 1951 and No. 50578, ad. sex ?, July 15, 1951.

Two old squaws were feeding in Salt Water Lagoon on June 17, 1952. On June 30, 1952, a nest of seven eggs was 20 feet from the edge of a lake at Umiat. One of the eggs was infertile and in the others embryos had barely begun to form. The nest was unattended but the eggs were warm and covered with down feathers. The next day the male was in the lake adjoining the nest and the female was on the nest; we collected the eggs on this date. The nest was in a natural depression in the moss on top of a hummock one foot high. A dwarf alder gave overhead protection.

Each night, at approximately 10:00 P. M. (July 3-11, 1952) a male lit in Wahoo Lake and preened, ruffled and adjusted its feathers. This behavior indicated to us that he had just been relieved from incubating eggs. Old squaws were noted also on a small lake approximately ½ mile southeast of Wahoo Lake on July 8.

Most of the old squaws (July 4-10, 1951) were in pairs or small groups at Topagaruk. They constituted less than one per cent of the avian population and were more commonly seen around the edges of stabilized lakes of medium size than elsewhere. One adult female shot on July 7, weighed 600 grams and had ova as large as 17 millimeters in diameter.

On July 8, 1952, between 1:00 A. M. and 2:00 A. M., the ice started to move and formed leads near the shore of the Arctic Ocean at Point Barrow. Ordinarily the ice does not leave until approximately the 20th of the month. These new leads brought greater numbers of old squaws nearer shore. At 6:00 P. M. that same day eighteen old squaw ducks sat on the ice off-shore and approximately 100 flew to the east in three separate groups.

At Kaolak River (July 12-18, 1951), old squaws were observed every day. On a four hour field trip (July 15), four adults were seen. On July 18 an old squaw was flying in company with a male pintail. An Eskimo hunting party of three men had killed a female (July 18) near our camp and were going to prepare it for food that evening.

At Kaolak (July 21-27, 1951) we observed one pair with young and two single adults.

At Barrier Lake, northeast of Teshekpuk Lake (July 29-Aug. 4, 1951), old squaw ducks were in evidence at least once or twice a day. On July 30, three birds were sitting on an island in a small lake adjoining Barrier Lake. They were molting and although capable of flight were using the island as a place of refuge. Two females shot on July 30, weighed 650 grams and had masses of ova smaller than those in the female shot at Topagaruk 23 days earlier. The largest ovum in the latter female was 2.3 mm in diameter. On a flight on August 4, 1951, from Teshekpuk Lake to Point Barrow we saw two flocks of 18 each when 73 and 34 miles southwest of Point Barrow.

Between the mouth of the Canning River Canyon and Umiat (July 18, 1952), old squaws were more numerous in lakes adjacent to the Colville River than in lakes to the east.

Upon our arrival at Gavia Lake (Aug. 20, 1952) a family of two adults and two juveniles and another family of one adult and six juveniles were the only ducks on the lake. One of the juveniles rested on the bank instead of feeding in the lake with the other ducks, and on August 23 died. On August 21, one duckling in the second family strayed out toward the center of the lake, whereupon the adult female swam out and herded the young bird back toward the group nearer the shore line. On August 22, the female and two ducklings of the first family were shot. The adult was 390 mm in total length whereas the young were 300 mm in total length and weighed 320 grams. Neither young birds nor the mother could fly. The breast of each young consisted of only a few thin layers of muscles whereas the adult's breast was made up of thick muscles. The second family had frequented the south shore, but moved to the north side of the lake when fired upon. On August 22, one duckling was 214 mm long and weighed 119 grams. Although the season was far advanced and the snows of autumn were already falling, ducklings of the sizes specified above were still unable to fly and the females were still molting the essential flight feathers.

At Driftwood (Aug. 30, 1952) an adult and two juveniles were feeding in a lake northeast of camp.

Polysticta stelleri (Pallas): Steller's eider. — Specimen, 1: Topagaruk, 155°48′, 70°34′, 10 ft., No. 30325, ad. female, July 10, 1951.

An incubating female was shot at Topagaruk on July 10, 1951. Her ovary was 30 mm long, and the largest ovum was 3 mm in diameter. Her nest was in a depression of a high-centered polygon some 300 feet from any large body of water, contained five fresh eggs, and was lined with black down feathers of an adult. On each of three occasions when approached, the female left the nest when I was six feet away.

On September 7, 1952, a flock of eight Steller's eiders was swimming in a large lake approximately one mile southeast of the Arctic Research Laboratory.

Somateria mollissima v. nigra Bonaparte: Common eider.—On August 25, 1952, approximately 100 yards southwest of Point Barrow, 30 Pacific eiders were resting on the beach in company with 90 king eiders. When approached some swam and others flew out onto the Arctic Ocean where they remained until we withdrew from the area, after which time the birds returned to their resting place on the beach.

PLATE 9

FIG. 1. A male yellow-billed loon setting on eggs in nest at Wahoo Lake on July 9, 1952.

FIG. 2. Nest and eggs shown in figure 1, July 9, 1952. Incubation had just begun.

FIG. 3. Arctic loon (upper) and red-throated loon (lower) from Teshekpuk Lake, August 1, 1951.

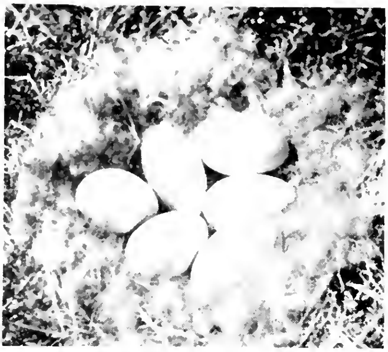

FIG. 4. Nest and eggs of white-fronted goose at Umiat, July 1, 1952. Incubation three fourths completed.

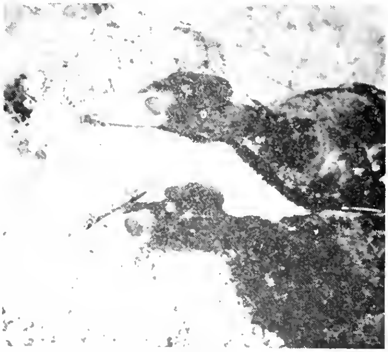

FIG. 5. Adult male surf scoters, July 16, 1952, at Porcupine Lake. Scoters are uncommon on the Arctic Slope.

FIG. 6. Arctic tern shot at Teshekpuk Lake on August 1, 1951. A common breeding bird in northern Alaska.

PLATE 10

FIG. 1. Shore of Arctic Ocean at Point Barrow, June 19, 1952. Many birds already were nesting on the tundra.

FIG. 2. Tundra and oriented lakes 80 mi. S Point Barrow, August 28, 1952, are breeding places for water birds.

FIG. 3. Luxuriant vegetation used by breeding birds in intermontane valley at Porcupine Lake, July 18, 1952.

FIG. 4. Willow-lined creek at Chandler Lake, August 25, 1951. Willows and alders offer nesting sites for birds.

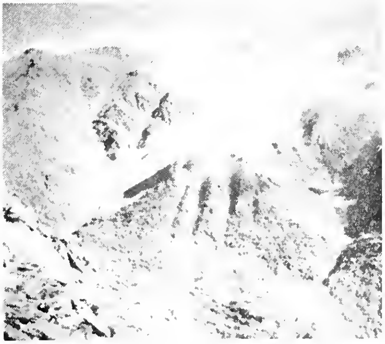

FIG. 5. NW face of Mt. Chamberlin, 9131 ft.; terrain inhospitable to most breeding birds. August 5, 1952.

FIG. 6. Destruction of bird communities by caribou trampling south of Lake Peters. August 8, 1952.

Somateria spectabilis (Linnaeus): King eider.—Specimen 1: Point Barrow, 156°27′25″, 71°23′11″, 3 ft., No. 31306, ad. male, August 25, 1952.

Robert McKinley told us that in the last week of April of 1952, eiders (king?) arrived in the vicinity of the Arctic Research Laboratory in large numbers and continued to pass to the east for the next three weeks. King eiders were observed at Point Barrow on July 3, 1951.

Ninety king eiders and 30 Pacific eiders were resting on the shore of the Arctic Ocean at Point Barrow on August 25, 1952. The following day 200 king eiders were in the same area. A male, shot there, measured 560 millimeters in total length. The muscles were only a third the size of those on a normal bird. Another eider found dead also was emaciated and may have died from gun shot wounds inflicted by the guns of the Eskimos. For every bird killed by Eskimos, several are injured; many of these die along the migration route. On July 28, king eiders were flying northwest along the shore of Elson Lagoon, thence across the Point Barrow Peninsula at Birnirk, and thence southwest along the coast of the Arctic Ocean. This day was foggy and wind was from the east. On clear days and especially when wind blows from the northwest, king eiders cross the peninsula a fifth of a mile or so nearer Point Barrow, which is the most northern extension of the Peninsula. More eiders moved by on clear days than on cloudy or foggy days. In one hour, ten flocks, averaging 400 birds each, passed overhead at Birnirk (July 28); three days earlier flocks of from 50 to 300 passed approximately every 20 minutes. Eskimos on this date were shooting into these flocks of eider and bagging them in excess of the winter needs of the hunters. One Eskimo had 40 king eiders undressed and hanging on a drying rod at his home at Barrow Village (Sept. 2, 1952).

On July 29, 1951, we flew from Point Barrow to Teshekpuk Lake and observed (2:00-3:00 P. M.) only two small flocks of king eiders. On August 1, 1951, at Barrier Lake, three large flocks were flying west beyond the north end of the lake. This was the first day since July 29, on which we had seen such large flocks so far inland.

On September 11, 1952, eight king eiders were resting on the shore of the Arctic Ocean at Point Barrow.

Lampronetta fischeri (Brandt): Spectacled eider.—On July 28, 1951, at Birnirk, several flocks were flying along the Arctic Ocean.

Melanitta perspicillata (Linnaeus): Surf scoter.—Specimens, 2: Porcupine Lake, 146°29′50″, 68°51′57″, 3140 ft., No. 31307 and 31308, ad. males, July 15, 1952.

Two males shot at Porcupine Lake on July 15, 1952, measured as follows: Total length, 489 mm, 495 mm; length of testis, 9 mm, 11 mm; weight, 1134 grams, 998 grams. These birds were frequently seen together along the south side of the lake. At Lake Schrader (July 27, 1952), 15 scoters, in loose groups of two to six, fed in the southwest corner of the lake.

Buteo lagopus s. johannis (Gmelin): Rough-legged hawk.—On July 2, 1952, a nest of three young approximately six days old was examined ½ mile southeast of Umiat Mountain. The young were being fed small mammals. Another nest containing three addled eggs was also examined near Umiat. Many infertile and addled eggs of several kinds of birds were noted on the Arctic Slope.

Aquila chrysaëtos canadensis (Linnaeus): Golden eagle.—Marvin Mangus told us that he had seen young in nests at the following localities: Kurupa River, 155°11′, 68°38′, on July 1, 1946; 10 miles south of Driftwood in latter part of June, 1950; 11 miles NW from the north end of Chandler Lake, 152°56′, 68°25′ on June 10, 1951; Awuna River, 157°03′, 69°12′ July 4, 1952. Single adult birds were seen by us at Gavia Lake (Aug. 21, 1952) and at Driftwood (Aug. 31, 1952).

Atanak and his companions from Wainwright saw 12 eagles while hunting (July 16-18, 1951) from the junction of the Avalik and Ketik rivers to a point seven miles up the Kaolak River, but no eagles were seen between the junction of the above rivers and Wainwright.

Golden eagles daily hunted prey along ridges where Arctic ground squirrels (*Spermophilus undulatus*) were abundant, for example, at Wahoo Lake (July 3-12, 1952) and at Porcupine Lake (July 13-18, 1952). This species of eagle hunted also in areas where marmots (*Marmota caligata*) were abundant, as on the slopes adjoining Lake Peters. There (August 6, 1952) three eagles soaring at 3800 feet elevation south of the mouth of Chamberlin Canyon elicited from each of four marmots three warning calls. Thereafter the marmots remained silent until the eagles had left the area. One eagle that consistently hunted (July 17, 1952) on the lower slope of Mount Annette along the Canning River was three times harassed by two ravens.

At the south end of Lake Peters (July 31, 1952), a pair of adult eagles soared along the slopes of Mount Mary approximately 1000 feet above the lake. Twenty minutes later these birds flew by camp at the base of the mountain. On August 2, at 8:00 P. M., two birds, one a large dark adult and one a bird of the year (?) dropped with partly closed wings from high on the east side of the lake to an undisturbed meadow on the west side. After circling the meadow once, the two birds spiralled upward to approximately 4500 feet elevation in one steep canyon, leveled off and after gaining the head of the next canyon, plummetted down to the base of the mountain some 1500 feet below. The high-speed flight continued across the ridge to the mouth of the next canyon where they circled twice and then soared upward to repeat the act. The objective probably was to surprise and prey upon small game at the mouths of each canyon. On August 13, the eagles were still in the area at the south end of Lake Peters in spite of an abrupt seasonal change; snow and rain increased and the temperature dropped.

On August 15, a Dall sheep (*Ovis dalli*) crossed the canyon from Mount Mary to the mouth of Chamberlin Canyon. As the sheep reached the east side of the canyon an eagle flew across the canyon and alighted approximately 150 feet from the sheep. A large group of small birds immediately harassed the eagle.

Two eagles fed on a dead caribou on a delta on the east side of Lake Peters. Eagles were noted every day at Lake Peters from July 31 to August 15 inclusive.

Falco rusticolus obsoletus Gmelin: Gyrfalcon.—At the southwest corner of Barrier Lake on July 29, 1951, a gyrfalcon sat on a bank 10 feet above the water level. A dead Arctic tern was on the beach only 90 feet away and visible to the gyrfalcon. When approached to within 250 feet, the gyrfalcon, rather than flying north over the lake and lowlands, flew south across the upland tundra. On August 3, on the edge of the upland tundra approximately 3½ miles farther east a gyrfalcon ate a Sabine's gull—a bird of the year. Its feathers had been plucked and only the stomach and intestines remained. The gyrfalcon left the feeding area when approached to within 450 feet and, as did the other gyrfalcon, flew south over the upland tundra rather than over the lowlands of inundated sedges. On July 4, one gyrfalcon sat on a promontory at the south end of Barrier Lake. This bird flew south.

At Umiat (Sept. 1-5, 1951) a gyrfalcon each day hunted the same areas of marsh in the river valley where tundra voles (*Microtus oeconomus*) were numerous and along the side of the valley where ground squirrels were common. On several occasions, this bird hovered 30 feet up and inspected us. This confidence was in contrast to that of the gyrfalcons at Teshekpuk Lake; they evaded us by leaving the ground several hundred feet away and flying out of sight.

Westley Redhead told us that a gyrfalcon was at Umiat as early as the latter part of May, 1952. We saw them there on September 1 and 2 in the same year. Gyrfalcons feed on ptarmigan in the river valley and on ground squirrels and small birds on the uplands by striking their prey on the ground. These falcons fly like prairie falcons and are of the same nervous disposition.

Falco peregrinus anatum Bonaparte: Peregrine falcon.—A nest was found on June 27, 1952, on the south slope of Mount Umiat approximately 225 feet above the Colville River, 40 feet from the top of the cliff and 30 feet west of the top of the mountain. The nest, three feet in depth at the front, two feet in depth at the rear, and 2½ feet wide was made of sticks of many years accumulation and was placed on a pinnacled platform 12 feet high. The nest contained one infertile egg and two others in which embryos were approximately one third developed. The female remained near us the one hour that we were in the area. She flew back and forth in front of the nest terminating each flight in an upswing arc and occasionally rested on top of the ridge to the west. She dove at us but never came closer than 10 feet before swerving upward. The male was not present. In a canyon ⅕ mile northeast of the nest two dead ptarmigan were at the edge of a willow cotton-grass swale. A nest of a peregrine falcon used three years before was 1⁷⁄₁₀ miles east and 1⁷⁄₁₀ miles north of Umiat. The nest was eight feet up on the face of a cliff 13 feet in height and easily accessible to either fox or wolf. Along the Colville River the falcon feeds on small shore-birds and other small birds.

Falco columbarius bendirei Swann: Pigeon hawk.—On a benchland between Chandler Lake and mountains to the west on August 12, 1952, a pigeon hawk hunted back and forth across a meadow, fearlessly inspecting us from distances of 20 to 30 feet as it searched the meadow for food. This falcon systematically searched those areas where longspurs were known by us to be most frequently found. Twice it flushed Lapland longspurs and darted at them but without success. Of the four pigeon hawks at Chandler Lake three were moving south and one was moving north down the canyon. We saw this species at Chandler Lake also on August 17, 20 and 21, 1951, and at Driftwood on August 27, 1952.

Approximately ¹⁄₁₀ mile north of James Robert Lake (Aug. 8, 1952) a pigeon hawk was harassing five ravens that were feeding on a dead caribou. This falcon flew back and forth above the ravens.

Falco sparverius sparverius Linnaeus: Sparrow hawk.—One seen in the summer of 1952 at the mouth of the Colville River by Clifford Fiscus.

Lagopus logopus alascensis Swarth: Willow ptarmigan. — Specimens, 5: Topagaruk, 155°48′, 70°34′, 10 ft., No. 50587, ad. female, July 8, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., No. 30586, ad. female, July 14, 1951 and No. 30585, ad. male, July 15, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., No. 30583, ad. male and No. 30584, ad. female, July 23, 1951.

Wherever ptarmigan were found, there was evidence that they were resident in the area throughout the year. At Topagaruk, informants said the ptarmigan were not so numerous in the summer (1949-1950) as in the winter. The apparent relative abundance of these birds in these two seasons could conceivably result from the birds being less conspicuous and more seclusive in the summer because of nesting activities. In summer these birds are protectively colored; at times a female only a few feet away is hardly distinguishable from the tundra. We observed only two adults and three juveniles in the area (July 5-10, 1952) although we saw considerable sign associated with the winter season. Sand dunes derived from material along the edge of the river formed a conspicuous feature of the landscape. These dunes, 20 to 30 feet high, were deeply cut by winds from the west-northwest. Ptarmigan tracks and sign were on all sides of the dunes, but the lee side was more commonly used than any other because of the protection from winds and the presence there of large willows and other plants. At Barrier Lake (July 29-Aug. 4, 1952) we noted numerous droppings of ptarmigan on the uplands between Barrier Lake and Teshekpuk Lake but we did not see any birds there. The sign could have been deposited either in the winter or in a previous season.

There are perhaps local migrations of ptarmigan. Harmon Helmericks, for instance, told us that in either April or May of 1946 he saw a ptarmigan on the ice of the Arctic Ocean 10 miles north of Pingok Island. At Gavia Lake (August 22) we observed a local shift of a group of ptarmigan. One day there were 19 birds in an area; the following day only seven birds were counted. On the third day the full complement of 19 birds were again in the area.

Ptarmigan are generally distributed on the Arctic Slope. On an airflight (July 3, 1952) from the mouth of the Canning River Canyon to Umiat the number of ptarmigan increased as we approached the drainage system of the Colville River. On this date, when these birds are nesting, the willows were just starting to grow new leaves and other vegetation of the tundra still was undeveloped. On August 16, along this same route, when young ptarmigan were nearly as large as adults, willows and alders were in full leaf and dominated the vegetation along water courses; the tundra was mature in appearance with considerably more green and yellow color in the landscape. The water in rivers and especially ponds was clear but brownish.

In the river valley at Umiat (June 28, 1952) a nest of seven eggs (½ incubated) was on an elevated mound supporting dwarf willow and birch averaging 1½ feet high. The nest was merely a concavity in sphagnum moss depressed by the weight of the bird. The female refused to leave the nest until bodily removed.

Dusting pits are actively used in the period of nesting. At Umiat (June 25, 1952), ptarmigan were using seven dusting pits on the shoulder of the airstrip. On the upland at Kaolak River (July 12, 1951), ptarmigan developed dusting pits on abandoned diggings made by Arctic ground squirrels. Most of the mounds were covered with mosses and lichens and other vegetation.

Individuals and family groups were noted at various localities on the Arctic Slope. At Kaolak River (July 15, 1951) on a four hour field trip, we saw three pairs of birds and their families of four to six young. One flock of eight adults was seen from the air at the mouth of the Canning River Canyon on July 22, 1952. At Kaolak (July 21-27, 1951) they were common; ten pairs of adults (males and female) were within a one mile radius of our camp. The families of young were in groups of 1-3-4-6-8-9-10-11-14. One group consisted of one male, two females and four young. While on a flight from Kaolak to Point Barrow (July 27, 1951) we observed several ptarmigan on the tundra. At Gavia Lake (Aug. 21, 1951) ptarmigan were in groups or singles as follows: two adult singles, group of seven young and one adult, group of four young and one adult and one group of five young and two adults. According to Harmon Helmericks, ptarmigan were high in population numbers on the Arctic Slope in 1952.

Ptarmigan were associated with most of the communities of the Arctic Slope but were noted more commonly in the following situations than elsewhere: At Kaolak (July 21-27) and at Kaolak River (July 21, 1951) in damp swales of grasses and sedges in poorly drained areas where soils were damp to supersaturated and among the dwarf willows bordering lakes and creeks; at Gavia Lake (Aug. 21, 1952) among willows and alders (4 feet high) along the edges of ox-bow lakes. On windy, cold days the ptarmigan were mainly on south exposures among grasses and sedges along lakes and on windless days were on flat tundra of polygons but near dwarf shrubs. On June 27, ½ mile northwest of Mount Umiat, two dead willow ptarmigan were noted along the edge of a willow and cotton-grass swale. The feathers had been plucked by a raptor (?) preparatory to his eating the ptarmigan.

Variations in parental display are indicated by the following observations. At Kaolak River (July 12) we flushed a family of adults and young. The male called as he left the ground and then he flew across the lake. The female, when flushed at a distance of 10 feet from the observer, feigned injury for 12 seconds before following the male. Seven young, averaging seven inches in length, left the ground and flew in the opposite direction from that taken by the male and female, to swales of cotton-grass and willow on the hillside. Another adult male and female were at the side of a young bird held in a trap. The female first left the young and fluttered over the vegetation for 40 feet and the male flew out of the area. Four other young were flushed 30 feet from the trap that held the captured ptarmigan. On July 17, while walking through a wet meadow of grasses and sedges, we flushed a male, female and four young (150 mm in length). The female crawled through vegetation for 30 feet and then rose into the air. At this same moment four young left the ground. The female, while in the air, reversed her course and joined the young, which had alighted some 300 feet away. On July 23, 1951, a family of two adults and 10 young were flushed. The male returned and chattered until the female arrived. The male then retreated 15 feet beyond the observer and remained close to the female while she tried to distract our attention from the young by pretending to have an injured wing. In a group of one male, two females and four young at Kaolak (July 21, 1951) the male and young left after the females fluttered along the ground for 30 feet.

Adults and young do not always escape by flying; on July 20, 1951, we were enroute from the landing lake to Kaolak when an adult male and female with eight young ran 200 feet down established tracks of a weasel vehicle. It was necessary to reduce the speed of the vehicle to spare the young. A male at Kaolak River (July 12, 1951) ran 150 feet under the protection of willows to an opening where it remained until flushed. It flew 50 feet, then alighted in another patch of willows.

At Gavia Lake at 11:30 P. M. a ptarmigan called because one of its young was caught in a trap at the edge of a lake. The juvenal bird, unharmed, was released and inadvertently was dropped into the water where it floated but finally, becoming confused, got its head and bill under water and drowned.

On July 15, 1951, at 11:00 P. M. at Kaolak River, we heard a ptarmigan joining an Arctic tern and several sandpipers in protest to a passing red fox.

For three consecutive days a family (male, female and young) at Topagaruk was within 50 feet of one place.

The following measurements of juveniles show increase in size as correlated with advance of season: Topagaruk (July 6, 1951) two juveniles averaging 110 mm in length weighed 21 grams; Kaolak River (July 17, 1951) young of one family averaged 178 mm in length and another individual was 162 mm in length and weighed 38 grams; Kaolak (July 21-27, 1951) individuals in a group of nine was approximately ¾ the size of parents and other groups were ⅓ to ⅔ the size of adults.

In a brooding female 600 mm long from Topagaruk (July 8, 1951) the largest ovum was two mm in diameter. Females, averaging 650 mm long from Kaolak (July 23, 1951) had ovaries smaller than the normal size for breeding birds; the largest ovum was only ½ mm in diameter. Males of the same size had testes six mm in length.

Lagopus mutus nelsoni Stejneger: Rock ptarmigan.—Specimen, 1: Wahoo Lake, 146°58′, 69°08′, 2350 ft., No. 31309, ad. male, July 11, 1952.

At Wahoo Lake (July 6, 1952), young of one brood for the first time since July 3, called continually throughout the day and part of the night. Members of three other broods, only a few days old, did not call in the same persistent way.

Along a deeply eroded western outlet of Wahoo Lake there was an unusual concentration of fecal droppings, spaced approximately every two or three feet. This sheltered place offered protection from cold and winds of winter. Adults were associated with willows along creeks and on adjoining sidehills where willows gave way to open tundra. One family left the willows and the female flew back and forth behind the young as she herded them. The largest adult male seen here was shot on July 11. It was 365 mm in total length, weighed 460 grams, and had testes 7 mm long.

At the south end of Lake Peters (August 14, 1952), a female and her two young, along with other kinds of birds, were attracted to our tent during snowstorms. On July 18 at Wahoo Lake, a juvenile was 200 mm in total length and weighed 100 grams whereas on August 9 at Lake Peters a juvenal male was 261 mm in length and 226 grams in weight.

Rock ptarmigan were uncommon at Chandler Lake. We observed the first bird in the area on August 22, 1952, 13 days after our arrival. Droppings of the birds were only occasionally seen there.

Grus canadensis canadensis (Linnaeus): Sandhill crane.—In 1952, two sandhill cranes called in the river valley north of Umiat on June 24. On June 26, 27 and 28, a single bird was seen there. It remained in the general area and called occasionally. Sandhill cranes are only occasionally seen along the Colville River. A pair of these cranes was seen near Meade River on August 16, 1952, by Marvin Mangus.

Charadrius semipalmatus Bonaparte: Semipalmated plover.—A pair of semipalmated plovers in company with their young along the edge of Seabee Creek at Umiat were seen on four consecutive days, July 18-21, 1952. A male and female measured, respectively, total length, 180 and 175 mm; weight, 50 and 55 grams.

Pluvialis dominica dominica (Müller): American golden plover.—Specimens, 10: Kaolak River, 159°47′40″, 70°11′15″, 30 ft., Nos. 30592-30596 including 2 ad. males and 3 ad. females, July 12, 14, 18, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., Nos. 30588-30591 including 3 ad. males and 1 ad. female, July 21-23, 1951; Umiat, 152°09′30″, 69°22′08″, 352 ft., No. 31312 of an adult of unknown sex, July 21, 1952.

On July 29, 1952, we noted a pair of golden plover 3/10 mile northwest of Umiat. At Kaolak River (July 12, 1951) golden plovers could be approached to within 80 feet and were less wary than black-bellied plovers at Topagaruk. When one bird was shot the mate remained near the dead bird.

At Kaolak (July 21-27) four families of plovers were within a radius of ½ mile of camp. Each of these families remained apart from the others whereas at Kaolak River the physiography of the terrain permitted the pairs to form social groups of several families of adults and young. At Kaolak males flew to meet any intruder and attempted to decoy the intruder while the female remained with the young, but at Kaolak River an observer would approach to within 80 feet of a nest or young whereupon the female feigned injury by fluttering her wings and moving on her belly in an effort to decoy the intruder, the male meanwhile remaining within 40 feet of the observer. At Kaolak River, birds stayed in the nesting or feeding territory until approached to within a hundred or so feet. Young birds (July 21) were approximately ¾ the size of adults. The largest bird collected at Umiat (July 21) weighed 155 grams and measured 26 mm in length. Five males, shot on July 12-23 at Kaolak and Kaolak River, averaged 144 (130-150) grams. The testes were 4.4 (4.0-5.0) mm long. Four females collected at the same time from this area, averaged 144 (140-150) grams. The ovaries were 7.7 (5.0-10.0) mm long and the largest ovum was 2.0 mm in diameter.

The call of the adult was two distinct curlewlike notes that differed from the slurred call of the black-bellied plover. Golden plovers can be decoyed by imitating their call.

At Barrier Lake, in a two hour field trip (July 29, 1951) we observed a flock of eight birds and one single; golden plovers were active there all day and night.

At Kaolak River (July 12, 1951) six pairs and their young were on open and exposed surfaces.

Squatarola squatarola (Linnaeus): Black-bellied plover. — Specimens, 2: Topagaruk, 155°48′, 70°34′, 10 ft., No. 30597, ad. male and No. 30598, ad. female, July 9, 1951.

At Barrier Lake, on July 4, 1951, two adults were feeding together in a bare lane which had been made and maintained by caribou. At Topagaruk on July 7, 1951, these plovers made up less than one per cent of the avian population. They were frequently on polygons having raised centers. Non-nesting or non-breeding birds were on bare wind-blown knolls adjacent to the river. On these knolls they fed with semipalmated sandpipers, pectoral sandpipers, and ruddy turnstones. On July 9, we visited polygons having raised centers and young called continually but we could not locate them. The call resembles that of the long-billed curlew but is more plaintive. Ordinarily these plovers kept beyond the range of our collecting gun but when one of the pair was killed the other, especially the male, remained near the dead bird until the collector approached to within 20 feet. Of a pair shot on this date the male weighed 207 grams and had testes 7 mm long; the female weighed 232 grams and the largest ovum was 3 mm in diameter. The species was recorded at Topagaruk from July 4 to 10, 1951, inclusive.

At the west edge of Smith Bay on July 29, 1951, while flying from Point Barrow to Teshekpuk Lake, we observed one group of approximately 40 black-bellied plovers flying along the edge of the lake. At Gavia Lake on August 21, 1952, two young were just able to fly but preferred to run on the ground.

Arenaria interpres interpres (Linnaeus): Ruddy turnstone.—Specimens, 5: Topagurak River, 155°48′, 70°34′, 10 ft., No. 30599-30603 including 4 ad. males and 1 ad. female, July 6, 8, 9, 1951.

Four males shot at Topagaruk July 6-9, 1951, weighed 105 (96-116) grams. The testes were 2.8 (2.5-3.0) mm long. A female from the above locality, shot on July 6, weighed 125 grams. These birds constituted less than one per cent of the avian population at Topagaruk and were more frequently on polygons with high centers and on high windswept knolls than elsewhere and were in company with black-bellied plovers, pectoral sandpipers and semipalmated sandpipers. One bird was observed on July 3, 1951, at ¼ mile southeast of the Arctic Research Laboratory at Point Barrow.

Capella gallinago delicata (Ord): Common snipe.—At Umiat (June 25, 1952) at 11:00 P. M. a female was sitting and calling from the top of a leafless alder tree some 210 feet from any favorable nesting grounds. A male was performing a nuptial flight overhead. Three other birds in the air were heard.

On July 13, 1952, at Porcupine Lake, we flushed a female from a damp meadow of grasses and sedges at the west end of the lake. She pretended to have a crippled wing. Seventy-five feet from this bird an abandoned nest and fragments of egg shells rested on top of a mound six inches from water and 10 feet from the west end of the lake. Two dwarf willows on top of the mound partly concealed the nest. Two days later (July 15), juveniles were caught in a line of traps set in this marsh. Four tree sparrows, one savannah sparrow and three species of small mammals also were taken from this marsh. At this time of year (July 15) all the terrain was free of snow and ice except that two patches of snow, one 8 x 12 feet and another 6 x 6 feet remained on the protected south shore of the lake and a few ice slivers remained in the deep crevasses on some mounds in the marsh. One bird was seen on August 13, 1952, in wet low polygons between Lake Schrader and Lake Peters.

Actitis macularia (Linnaeus): Spotted sandpiper.—At the south end of Lake Peters on August 15, 1952, after snow covered the valley, a juvenal spotted sandpiper remained along the shore line nearer camp than it had been for four previous days.

Heteroscelus incanum (Gmelin): Wandering tattler.—On each of the days July 3-11, 1952, a wandering tattler was flushed from dense high willows along an 8-foot-deep creek channel that carried water from the west end of Wahoo Lake into the East Fork of the Ivashak River. The bird was at home in the willows and had considerable dexterity in perching on limbs. Although the bird favored one section of the creek, an exhaustive search for young, eggs or nest was fruitless. A loud call was given by this bird when disturbed.

Erolia melanotos (Vieillot): Pectoral sandpiper.—Specimens, 52: Barrier Lake, NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., 33, Nos. 30616-30636, 30638-30648, 30754 including 5 ad. males, 12 juv. males, 1 ad. female and 15 juv. females, July 30, Aug. 1-3, 1951; Topagaruk, 155°48′, 70°34′, 7, Nos. 30649-30655, including 3 ad. males and 4 ad. females, July 6, 8, 9, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 6, Nos. 30610-30615 of ad. females, July 12, 14, 15, 18, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., 6, Nos. 30604-30609 including 1 juv. male and 5 ad. females, July 20-23, 1951.

The earliest record of young (135 mm in length and 26 grams in weight) was at Kaolak River on July 14, 1951. On July 9, 1952, at Topagaruk the oviduct of an adult female, 86 grams in weight, contained an egg in a shell 200 mm in diameter. Her second largest ovum was 10 mm. Breeding males on this date had testes averaging 11 mm in length. The average length of testis of 15 juveniles shot on August 3, 1951, at Teshekpuk Lake was 1.9 (1.5-2.0) mm. The average weight of these juveniles was 60 (50-81) grams. A comparison of male and female juveniles shows no significant differences. Nevertheless, adult males in both the breeding and post-breeding seasons are longer bodied and heavier than adult females.

In the period June 14-25, 1952, in the Point Barrow area, pectoral sandpipers were puffing their throats and cooing. On June 23, several birds were defending territories, and one half mile northeast of Barrow Village (June 23, 1952) we noted a male pectoral sandpiper that crouched low when a pomarine jaeger flew directly overhead. After the jaeger passed, the sandpiper assumed normal posture and continued feeding.

At Topagaruk (July 7, 1951) these birds represented less than one per cent of the avian population, were common on polygons having low centers, and frequently joined black-bellied plovers, ruddy turnstones, and semipalmated sandpipers to form discrete flocks.

On a four hour field trip at Kaolak River (July 15, 1951), the pectoral sandpipers (45 by actual count) were the most common of the sandpipers and were always calling overhead. The young on this date were not yet capable of flight and were being fed by adult females. One of the immatures bathed in water at the edge of the beach. On July 18, females were still attempting to decoy intruders by pretending to have broken wings. Eight adults with young were observed at Kaolak (June 21-27, 1951) but the species was not so aggressive as at Kaolak River, nor so numerous. The fewer birds may have been correlated with lack of sand dunes, river beaches and open areas.

A group of five pectoral sandpipers frequented the shore of Barrier Lake (July 29, 1951) but the group was not seen the following day. On August

3, there was a sudden increase of pectoral sandpipers in the area; most of them were in flocks of six to 50. From one point along edge of the uplands, we shot 20 birds from several different flocks consisting mostly of juveniles. They seemed curious about our presence. When a bird was shot from the flock, the entire group circled back and forth over the dead or injured bird, sometimes only three or four feet above our heads. In the late evening of this same day, the number of pectoral sandpipers increased and although some were moving westward, most of them were moving eastward. On the following day they were still present in great numbers. The day before the arrival of these migrating birds, two adults (Aug. 2) acted as if they were still attending young. On July 30, we shot at a lone bird as it flew by and thereupon it climbed upward until nearly out of sight as they frequently did when chased by falcons.

At Lake Schrader (July 23, 1952) pectoral sandpipers were active 24 hours of the day.

On August 4, 1952, at the south end of Lake Peters, a group of eight pectoral sandpipers fed near camp. On August 5, one was shot and on the following day only seven were seen, suggesting that they were established in the area and were not migrants. They left on August 12.

At James Robert Lake (3600 feet elev., August 8, 1952), which is the most southern body of water in the canyon south of Lake Peters, several pectoral sandpipers were feeding along the edge of the lake and on the alluvium outwash below James Robert Glacier.

At Gavia Lake there was a decided trend in movement of groups of pectoral sandpipers. On August 22, 1952, groups of 2, 4, 6, 8, 8, 8, 16, 17, 18 flew by to the east. The day before there were only a few sandpipers and these were not especially on the move. Comparison between dates of active movements of sandpipers in 1951 and 1952 indicate that migration was considerably earlier in 1951 than in 1952.

Erolia bairdii (Coues): Baird's sandpiper.—Specimens, 5: Topagaruk, 155°48′, 70°34′, 10 ft., 4 Nos. 30657-30660 including 2 ad. males and 2 ad. females, July 7, 9, 10, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 1, No. 30656, ad. male, July 12, 1951.

On June 14, 1952, at Birnirk mounds, when snow still covered most of the ground, Baird's sandpipers were already established on territories. A nest of four eggs was examined ¼ mile southeast of the Arctic Research Laboratory on July 4. The female left the nest when the observer approached to within 20 feet and flew directly toward him and then dropped to the ground and pretended to have a broken wing. We pursued this bird for 50 feet before she took flight. The male, which flew at a much greater speed than the female, was nearby and soon joined her in flight. The female repelled her mate by chasing him, but the male persisted in accompanying her. If one or more males of this species (on one occasion as many as five) approached the territory of these nesting birds, the male would leave the female and chase the trespassers. On one occasion, after we left the nesting area, the female returned to the nest after approximately four minutes. Her approach to it was direct and without hesitation. After ½ hour we returned to the nest and the male was standing one foot away from the brooding female with his head resting on his wing. The male, followed by the female, left the nest and feigned injury. Shore-birds and water birds were more numerous on this date on the tundra and lakes nearer the Arctic Ocean (in the Point Barrow area) than in the direction of the Brooks Range.

At Topagaruk (July 5-10, 1952) adults of this species were the fourth most common bird, representing four per cent of the avian population. They were near lakes among polygons some of which had low centers whereas others had high centers. One bird had a nest and four eggs approximately 150 feet from an oil derrick, surrounded on all sides by the tracks of vehicles. This bird feigned injury at the nest notably more than did Baird's sandpipers that inhabited undisturbed tundra beyond. Three adult males, shot at Topagaruk (July 7-10, 1951), averaged 44(42-47) grams in weight and had testes averaging 3.5(3.0-4.5) mm long. Two females, collected in the same period and at the same place averaged 44 grams in weight. The largest ovum was one mm in diameter and the largest ovary three mm long.

Other occurrences were: Kaolak River, July 12-18, 1951 (four juveniles observed in one four hour field trip July 15); Lake Schrader, July 24-28, 1952; Point Barrow, July 27, 1951 (most common shore-bird at fresh-water ponds adjacent to the Arctic Ocean); 2 mi. S Wahoo Lake, on a high divide between the Ivashak and Sadlerochit rivers, July 8, 1952; Lake Schrader, July 23-31, 1952 (active at all hours); S end Lake Peters, August 1 and 2 but not seen there later.

Erolia alpina pacifica (Coues): Dunlin.—Specimens, 21: Barrier Lake, NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., 1, No. 30661, ad. male, Aug. 1, 1951; Topagaruk River, 155°48′, 70°34′, 10 ft., 20, Nos. 30662-30681, 12 ad. males and 8 ad. females, July 6-9, 1951.

Specimens shot at Topagaruk River (July 6-9, 1951) yielded weights of 57(53-64) grams for eleven adult males and 59(55-65) grams for six females. Testes were 3.5(2.0-5.0) mm long, the largest ova were 1.2(.5-2.0) mm, and ovaries were 3.5(3.0-4.0) mm long. An adult female from Teshekpuk Lake (August 1, 1951) weighed 48 grams. Her largest ovum was one mm in diameter and the ovary was 3.5 mm long.

At Topagaruk we observed the species every day (July 5-10, 1951) and on July 7, located a nest and four eggs. Each of the seven times that the brooding female was approached she left the nest when we were approximately 80 feet away and she flew approximately 150 feet before alighting at which time she called. The call resembled that of the western grebe. The wary nature of this sandpiper was in contrast to that of the other smaller shore-birds; they left the nest only when almost stepped on. On July 9, the nest still held four eggs. Adults were the fifth most common bird and made up three per cent of the avian population. They frequented polygons having low centers adjacent to stabilized lakes. At Kaolak River (July 17, 1951) a dunlin was feeding and flying with a group of four semipalmated sandpipers. At Point Barrow (July 27, 1951) dunlins were congregating in small groups at ponds and small lakes adjacent to the Arctic Ocean. At Barrier Lake (July 29-Aug. 4, 1951) three dunlins fed in the area but did not show territorial behavior.

Limnodromus scolopaceus (Say): Long-billed dowitcher.—Specimens, 5: Topagaruk River, 155°48′, 70°34′, 10 ft., 2, Nos. 30687, ad. male, July 7, 1951 and 30688, ad. female, July 8, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 3, Nos. 30684-30686, 3 ad. males, July 12, 14, 1951.

Four males shot at Topagaruk and Kaolak River (July 7-14, 1951) averaged 104(100-110) grams in weight and had testes 4.7(4-6) mm long. An adult female (July 8) from Topagaruk, weighed 130 grams and her ovary was 7.8 mm long. Her largest ovum was 3.5 mm in diameter. A juvenile from Kaolak River on July 14, 1951, was 150 mm in length and weighed 28 grams; thirteen days later, at Kaolak, a juvenile was shot that measured 265 mm in length and weighed 70 grams.

At Kaolak on July 15, 1951, we saw eight pairs of adults in a four hour field trip. Their young were approximately ½ grown. One pair of adults and four young, the size of parents, were seen daily in the same general area at Kaolak (July 21-27). One bird was observed on August 4, 1951, at Teshekpuk Lake.

Ereunetes pusillus (Linnaeus): Semipalmated sandpiper.—Specimens, 28: Barrier Lake, NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., 4, Nos. 30692-30695 including 3 juv. males and 1 juv. female, July 30, August 1, 3, 1951; Topagaruk River, 155°48′, 70°34′, 10 ft., 21, Nos. 30682, 30683, 30696-30714 including 12 ad. males and 9 ad. females, July 6-9, 1951; Kaolak River, 159° 47′40″, 70°11′15″, 30 ft., 3, Nos. 30689-30691 including 2 ad. males and 1 ad. of unknown sex, July 12, 14, 15, 1951.

Eleven adult males and nine adult females shot at Topagaruk from July 5-10, 1951, weighed 29(22-30) and 28(25-31) grams, respectively. The greatest length of skulls of each of the above sexes averaged 39.2 mm. The shortest juvenile, having a skull measuring 35.9 mm long, was a male shot at Kaolak River on July 15, 1951. Juveniles shot at Teshekpuk Lake on August 1 and 3, 1951, averaged 25 grams in weight and 28.4 mm in greatest length of skull. Testes of adults decreased in size from an average of 4 mm on July 6, to an average of 2 mm on July 14. Testes of juveniles on August 3 averaged 1.3 mm in length. The ovaries of seven adults from Topagaruk, shot on July 8 and 9, averaged 2.4 mm in length and the average diameter of the largest ovum was 7/10 mm.

A nest of four eggs, first examined on July 5, 1951, ¼ mile southeast of the Arctic Research Laboratory, was abandoned on July 11.

At Topagaruk (July 7, 1951) we flushed several adult semipalmated sandpipers whose behavior suggested that they were nesting. Two days later one nest held newly hatched young. This species was third in abundance there, adults constituting 15 per cent of the avian population. They were numerous on polygons having low centers and on high windswept knolls in association with black-bellied plovers, ruddy turnstones and pectoral sandpipers. The call resembled that of the Hammond flycatcher and was accompanied by wing vibration.

At Topagaruk (July 9, 1951) a female semipalmated sandpiper fluttered off a nest, uttered a sharp cry, feigned injury by fluttering around the observer, became seemingly indifferent but refused to return to her nest, uttered sharp cries, came to within seven feet of the observer who was sitting within three feet of the nest and alternately chattered, ate several large dipterous insects from the ground and in approximately five minutes went back on the nest, within easy reach, although she still was not completely quiet. When the observer rose to leave she again fluttered off the nest and feigned injury (the bird was preserved as a specimen). The nest was concealed in a small depression surrounded on all sides by tufts of vegetation and contained four young, one of which had hatched no more than three hours before.

On a four field trip at Kaolak River (July 15, 1951) we counted 14 juveniles in large stands of willows among sand dunes. These juveniles were making short flights of from 15 to 40 feet. In contrast to the situation at Topagaruk (July 5-10), there were fewer semipalmated sandpipers than Baird's sandpipers at Kaolak River (July 12-18, 1951). July 16 was the first date on which family groups of sandpipers here ventured out on the exposed sand bars along the river for feeding. One juvenile was carried by wind over the river where it dropped into the water. When last seen the juvenile was being floated upstream by the wind. Next day in the same general area where winds had driven water on the sand, four semipalmated sandpipers were feeding with dunlin. These five birds kept together both on the ground and in flight.

At Point Barrow (July 27, 1951) semipalmated sandpipers were forming small groups and feeding on small lakes and ponds adjacent to the Arctic Ocean. At the south end of Lake Peters (Aug. 3, 1952) several semipalmated sandpipers were feeding in dry areas of alluvium trampled by caribou.

Limosa lapponica baueri Naumann: Bar-tailed godwit.—At Kaolak River on July 18, 1951, one godwit was in company with a pair of golden plovers on a bare slope of an old sand dune along the edge of the river. The godwit when approached flew 150 feet and alighted and when pursued again flew another 150 feet and then departed for a lake ⅕ mile away.

Phalaropus fulicarius (Linnaeus): Red phalarope.—Specimens, 11: Topagaruk River, 155°48′, 70°34′, 10 ft., 11, Nos. 30715-30725 including 10 ad. males and 1 ad. female, July 6-9, 1951.

At Topagaruk (July 5, 1951), we located a nest and four eggs on the edge of a small drainage channel on the tundra. The nest was among mosses and lichens, one foot from open water. The bird left the nest when the observer was only four feet distant but on a second approach one hour later, left when the observer was 20 feet away. In each instance the bird pretended to have an injured wing. On July 7, this nest held four eggs. On July 8, there were four young, hatched either the previous afternoon or night and the female left the nest when the observer was 30 feet away. Ten adult males, shot at Topagaruk (July 5-10, 1951), averaged 50(45-54) grams in weight. These birds had testes that averaged 6.5(2.5-9.0) mm long. The red phalarope on July 7 was the fifth most common bird in the area, making up two per cent of the avian population and was commonly seen on polygons having high centers.

At Kaolak River (July 12-18, 1952) red phalaropes were uncommon. On July 15, a female was noted but seemed not to have young or to be nesting. A juvenile from Kaolak (July 22, 1951) was 180 mm in length and weighed 31 grams. On September 6 and 7, we observed hundreds of these birds, mostly juveniles, feeding in the ocean two to three feet beyond beaches at Point Barrow. Small lakes and open water in marshes had been frozen over since September 5, but larger lakes still were open. Except for a few birds around edges of open bodies of water, the great bulk of red phalaropes was (Aug. 7, 1951) on the Arctic Ocean. On September 11, there was none at Point Barrow. Thomas Brower, a resident at Barrow Village, stated that he had never before seen this species congregate on the Arctic Ocean bordering the shore.

Lobipes lobatus (Linnaeus): Northern phalarope.—Specimens, 5: Topagaruk River, 155°48′, 70°34′, 10 ft., 2, Nos. 30729, ad. male, July 9, 1951, and 30730, ad. female, July 8, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 3, Nos. 30726-30728 including 2 ad. males and 1 ad. of unknown sex, July 14, 15, 1951.

In the period July 8-15, 1951, four adult males at Topagaruk and Kaolak River averaged 31(28-33) grams in weight. Their testes averages 2.3(2-3) mm long. A female (July 8) weighed 37 grams. Her largest ovum was 2 mm in diameter. A juvenile from Kaolak River (July 16) was 176 mm long and weighed 35 grams. Young northern phalaropes at Kaolak River (July 12-18, 1951) were more numerous than at Topagaruk (July 4-10, 1951) and were almost the size of adults. On July 15, on a four hour field trip, we counted 24 individuals including adults and juveniles. On this date the juveniles were almost ready for flight. At Kaolak (July 22, 1951) a young bird 212 millimeters in length was flying and feeding alone. In our seven day stay at Teshekpuk Lake only one northern phalarope was seen. It was near camp on August 3, 1951. Between Birnirk and Point Barrow (Aug. 25, 1952), approximately 3000 northern phalaropes had collected on fresh water ponds, salt water lagoons and on the Arctic Ocean. Many of them were feeding while others were nesting on matted green mosses bordering ponds. Their habit of spinning in water was noted. Those feeding on the Arctic Ocean were on the relatively smooth water immediately beyond the point where the breakers formed. On September 11, at Point Barrow, we did not see the species.

Stercorarius pomarinus (Temminck): Pomarine jaeger.—At Birnirk (June 14, 1952) while snow still covered most of the ground, pomarine jaegers hunted for lemmings by flying approximately 20 feet above the tundra and occasionally hovering. On June 15, one had eaten parts of two large lemmings caught in traps along the edge of a snow-bound lake. On June 17, these birds were preying on live lemming and swallowing them whole. One flew 50 meters with a brown lemming in its mouth and after alighting, consumed it. The backs of several lemmings caught in traps had scars probably made by jaegers or conceivably by snowy owls. West of Salt Water Lagoon (June 17, 1952), 12 jaegers were counted with the aid of a 6 x 30 power binocular in a 90° arc to the southward. Three snowy owls also were hunting in this area. In traveling one and three-eighths miles south by east from Barrow Village on June 20, 1952, we counted eight single pomarine jaegers in the air and on the return trip the same day, five pomarine jaegers (one was dead, another was resting on a lake and 3 were in flight).

At Point Barrow (June 21, 1952) two pomarine jaegers left the land and flew north out of sight over the Arctic Ocean. At a point 9/10 mile east and 4/5 mile north of Barrow Village (June 23, 1952) we observed a pomarine jaeger cruising three feet above ground. It dropped to the tundra and picked up a lemming by its back and after adjusting the lemming swallowed it tail first. On a lake one mile southwest of the Arctic Research Laboratory a group of six and two pairs all facing into the wind were resting on ice. In an area of 240 acres (outlined by the tripod communication line to the west, "Y" line to east, and row of 50 gallon drums following the ground line to south), we counted 19 pomarine jaegers in groups of from one to four or one per 12 square acres; one snowy owl was in the area.

At Kaolak River (July 12-18, 1951) pomarine jaegers were the second most common jaeger in the area. In walking for four hours on July 15, two pairs were noted. Ordinarily, however, these birds are seen singly not in pairs. At Lake Schrader (July 23-31, 1952) pomarine jaegers were active both day and night, especially at night. At Barrier Lake (Aug. 2, 1951) two pomarine jaegers flew close together along the edge of the south end of the lake. As they left the lake and flew over the extensive marsh to the east they separated and flew as single individuals. On August 4, a pomarine jaeger was chasing an Arctic loon that had a fish in its bill. On August 10, 1951, a single pomarine jaeger was noted at Chandler Lake. As late as September 7, 1952, one half mile south of the Arctic Research Laboratory, seven pomarine jaegers were foraging for brown lemmings.

Stercorarius parasiticus (Linnaeus): Parasitic jaeger.—Specimens, 3: Topagaruk River, 155°48′, 70°34 , 10 ft., 2, Nos. 30732-30733, ad. females, July 6, 8, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., 1, No. 30731, ad. male, July 21, 1951.

At Topagaruk (July 5-10, 1951) parasitic jaegers ranged over nearly all plant and animal associations, but flew more frequently over polygons with low centers than elsewhere. Data on two adult females, shot on July 6 and 8, in that order are as follows: weight, 525, 320 grams; largest ovum, 3, 1 mm; length of ovary - - -, 5.5 mm. The bird killed on July 6 was in the black color phase.

At Kaolak River (July 12-18, 1951) the parasitic jaeger was the least common of the three species of jaegers.

At Kaolak (July 21-27, 1951) two birds nested near camp while others passed through the area. These passing birds generally were seen singly or in pairs; long-tailed jaegers commonly are in groups of four or five. The parasitic jaegers were not so noisy nor so much given to chasing others of their own species as were long-tailed jaegers. Several single birds hunted in areas of sedges and grasses that yielded lemmings. On July 21, a parasitic jaeger was flying with three glaucous gulls, and demonstrating its usual flight tactics of gliding, climbing and swooping as it accompanied the gulls. An adult male shot on July 21, weighed 460 grams.

On alluvial outwash at the southwest end of Lake Schrader (July 27, 1952) a male and female parasitic jaeger defended their territory by diving at us. Periodically both birds alighted approximately 60 feet away and each pretended to have a crippled wing for approximately a minute. The female acted as if herding the young but was not. On each of our daily inspections an adult defended the area. In a period of four days the area defended was shifted approximately ⅕ of a mile south in the marsh area adjacent to the lake. Parasitic jaegers were noted in the Lake Schrader area from July 23 to July 31 inclusive.

At Barrier Lake (July 30, 1951) two parasitic jaegers were harassing a glaucous gull that responded as if being attacked by a hawk. The plunging of the jaeger continued while the gull was flying 300 feet horizontally. One other jaeger chased a glaucous gull for one-fourth of a mile and finally having caught up with it dove at the gull several times, each time almost making contact. From our camp on Barrier Lake (July 29-Aug. 4, 1951) we watched parasitic jaegers hunt along the south end of the lake, following precisely the edge of the water. The wind drove debris to the south end of the lake. The long-tailed jaeger was the more numerous here; it flew along ridges and over marshes. On July 30, a single jaeger flew over the lake and after hovering above a young Arctic loon, which had strayed from its parent, dove down and picked it up. Three other parasitic jaegers arrived and competed for the prey.

A single parasitic jaeger was noted at Chandler Lake on August 10 and one on August 11, 1951. At Gavia Lake (Aug. 21, 1952) there were six jaegers in one group.

Stercorarius longicaudus Vieillot: Long-tailed jaeger.—Specimens, 5: Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 1, No. 30738, ad. female, July 12, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., 4, Nos. 30734-30737 including 2 ad. males and 2 ad. females, July 21, 1951.

The long-tailed jaeger was the second most abundant of the three jaegers at Topagaruk (July 5-10, 1951). The greatest number seen on any one day was three. At Kaolak River (July 12-19, 1951) this species was the most common jaeger. On a four hour field trip (July 15 and 18) we saw six birds. When in groups of three or more, they frequently chased each other and called vigorously. One adult female shot on July 12, weighed 300 grams. The largest ovum in the female was 1.2 mm in diameter and the ovaries were 5 and 6 mm long.

Within ⅕ of a mile of our camp at Kaolak (July 21-27, 1951) there were three breeding pairs of jaegers. On a four hour trip beyond this limit we saw as many as 14 individuals. Most of these were in groups of three and were commonly seen flying over meadows and along ridges. Single birds hunted by hovering or swinging upward. Territories vacated by our collecting adult birds were not immediately filled by other nesting jaegers. One pair of jaegers nested in a broad grassy meadow. The female was aggressive and demonstrative and called continually above her young. The male was less demonstrative but joined the female when she began calling. On July 24, four jaegers flew over areas where brown lemmings had been trapped in greatest numbers. Two adult males shot on July 21, weighed 270 and 250 grams. The testes of these two birds were 5.5 and 8.0 mm long. Two adult females from the same area, and shot on the same date as the males, were larger than the males. The females weighed 285 and 298 grams.

At Barrier Lake (July 29, 1951) we observed three long-tailed jaegers, all chasing and harassing a glaucous gull. These jaegers hunted mostly along ridges and over marsh. At midnight these birds were still hunting and flying about. Other long-tailed jaegers were on the lake from July 29 to August 4 inclusive.

At Gavia Lake (Aug. 21-23, 1952) two long-tailed jaegers fed from our refuse pile only 30 feet from our tent. A single individual was noted at Lake Peters on July 25, 1952, and one at Driftwood on August 27, 1952.

Larus hyperboreus barrovianus Ridgway: Glaucous gull.—Specimen, 1: Topagaruk, 155°48′, 70°34′, 10 ft., No. 30739, ad. male, July 9, 1951.

Robert McKinley told us that on May 16, 1952, approximately 25 gulls, probably glaucous gulls, arrived at the Arctic Research Laboratory and remained until May 25. On July 4, 1951, there, we recorded all gulls passing over the ice from 8:45 A. M. to 9:45 A. M. At this time the shore line and first 100 feet of water was free of ice; beyond, seaward, the ice was rough and dark for ¼ mile, succeeded by white ice for ¼ mile, next the high pressure ridge, and then open water of the Arctic Ocean. Glaucous gulls, singly, passed to the southwest and to the northeast at intervals of 6(3-10) minutes at a distance of 500(300-800) feet from the shore line, except for one bird that was approximately one mile off-shore.

On July 10, 1952, off-shore from the Laboratory, where garbage from camp was deposited on the ice, approximately 130 glaucous gulls were present—some resting on the ice and some flying. At six P. M., four hours later, 84 gulls including several immatures remained. Birds in groups were constantly walking about or flying short distances, but lone individuals stood perfectly still for long periods. On July 11, only 22 birds remained; they were flying up and down the shore line. At Topagaruk (July 5-10) glaucous gulls fed on the refuse pile at camp. The number varied from day to day, from as few as 10 to as many as 22; a few remained at the feeding grounds at all times.

The testes of an adult male (30739), shot on July 9, 1951, at Topagaruk were 15 mm long and 9 mm thick.

At Kaolak River (July 12-19, 1951) gulls occasionally cruised up or down the river, but did not remain in the area. When we flew from the mouth of Canning River Canyon to Umiat (July 16, 1952) the only glaucous gulls noted were in the vicinity of the Colville River. At the Will Rogers Monument 12 miles southwest of Barrow Village (July 18, 1951), 275 glaucous gulls were at the mouth of one of the streams entering the Arctic Ocean, and 50 miles southwest from Point Barrow along the ocean six gulls flew over the water where a muddy stream from the land was discharging into the Arctic Ocean. On July 20, 400 of these gulls were near the Arctic Research Laboratory and in the large lake southwest of camp. At Kaolak (July 21-27, 1951) five to eight birds remained near camp. Along the larger creeks they flew by approximately every two hours.

On an air trip along the Arctic Ocean 56.2 miles southwest of Barrow Village (July 27, 1951) we counted 312 gulls, most or all glaucous gulls, in small groups as follows: average size of flock, 34(2-70); average distance between flocks, 5.8(1.9-13.6) miles. A large flock of 188 glaucous gulls, on this date, was in the environs of Barrow Village and the Arctic Research Laboratory. On an airflight between Point Barrow and Smith Bay (July 29, 1951) we observed three groups (1-2-7) equally spaced between the two points. The glaucous gulls were seen in only small numbers at Barrier Lake (July 29-Aug. 4, 1951) generally as individuals or groups of two or three, and frequently were harassed by jaegers. On August 3, a glaucous gull on three occasions inspected but did not touch a freshly killed pectoral sandpiper floating on the surface of the water. On a flight from Teshekpuk Lake to Point Barrow (Aug. 4, 1951) we observed groups of gulls as follows: one at 40 miles (miles are from Point Barrow), four at 34 miles, four at 10 miles and twenty-three at 8 miles. At Driftwood (Aug. 27-31, 1952) groups of from one to 12 glaucous gulls were seen every day. At Umiat (Aug. 30-Sept. 4, 1951) several birds were flying up and down the river. In 1952 (July 18) at 10 miles east of Umiat we observed a single bird. On August 25, 1952, at Point Barrow, 33 glaucous gulls few along the edge of the Arctic Ocean. Between Birnirk and Point Barrow (Sept. 11, 1952) a group of 230 glaucous gulls rested along the shore of the Arctic Ocean. Glaucous gulls were noted also at the following places in the Point Barrow area (1952): west side Salt Water Lagoon, June 17; 9⁄10 mile east and 8⁄10 mile north Barrow Village, June 23; 1 mile southwest Barrow Village, September 6; ½ mile south Arctic Research Laboratory, September 7.

Larus canus brachyrhynchus Richardson: Mew gull.—Specimens, 2: SE Lake Peters, 69°20′56″, 145°09′26″, 2950 ft., 1 imm. female No. 31314 (Aug. 6, 1952) and one adult female 31313 (Aug. 9, 1952).

At the southwest end of Lake Schrader, from July 23 to 31, 1952, a pair of mew gulls defended a territory and two young in the marsh bordering the edge of the lake and flew to meet us whenever we approached. They were active day and night. On August 3, 4, and 5, the female of this pair fed at the mouth of the river that flowed into the south end of Lake Peters 4.9 miles south of the nesting territory. On August 6, both adults and the two juveniles were at the south end of Lake Peters. The young called frequently and the adults, when we came near their young, called loudly and dived at us, but remained higher in the air than they did when protecting their young on the nesting territory. On August 6, the female (435 mm long and 290 grams in weight) was shot and prepared as a specimen. The two juveniles and the male remained in the area and on August 9, one of the juveniles (female) 422 mm in length and 362 grams in weight, was shot. On August 12 the male and one juvenile were still in the same area, and active day and night.

Pagophila eburnea (Phipps): Ivory gull.—Pete Savolik told us that whenever the pack ice came near shore at Point Barrow, a few ivory gulls were generally present.

Rissa tridactyla pollicaris Ridgway: Black-legged kittiwake.—Specimen, 1: 7½ mi. S and 7 mi. W Point Barrow, 156°49′, 71°17′, sea level, 1 (skin) No. 31315 of an adult of unknown sex, September 6, 1952.

The kittiwakes (Sept. 6, 1952), were in the air along the Arctic Ocean at Barrow Village and all along the coast at least as far as a point 10 miles southwest of Barrow Village (only a few were seen northeast of Barrow Village) and were feeding on material floating in the pre-breaker area of the ocean and to a lesser extent on debris washed up on the sands of the beach.

Xema sabini sabini (Sabine): Sabine's gull.—Specimens, 8: 7½ mi. S and 7 mi. W Point Barrow, 156°49′, 71°17′, sea level, 1 (skin) No. 31316, ad. male, Sept. 6, 1952; Topagaruk, 155°48′, 70°34′, 10 ft., 7 Nos. 30740-30746 including 4 ad. males and 3 ad. females, July 6, 8, 9, 1951.

At Topagaruk the species was seen daily from July 4 through July 10, 1951. Six adults were nesting on July 5. They constituted less than one per cent of the avian population inhabiting stabilized lakes of medium size. On July 8, one nest held young. When we approached the nesting grounds they flew 150 feet to meet us and then returned, hovered, or flew directly over their nests. One nest was on an island one foot in diameter; other islands inhabited were as large as one square meter. The vegetation at the nest was bright green and lawnlike because of trampling and fertilization of the grasses and sedges by the birds. Correspondingly green, lawnlike areas of grass were noted on the resting grounds of ducks and geese. The Sabine's gull and Arctic tern are compatible and nest within 20 feet of each other. The young freely circulate through each other's territory. The average weight of three adult males (July 6-8) was 202(190-214) grams. The average length of the testes of these birds was 10(8-14) mm. Four adult females collected at the same place and time weighed 177(158-190) grams. The ovaries averaged 8 mm long and the largest ovum was 2.8(2.0-4.5) mm in diameter.

At Kaolak River on July 17, 1951, one gull flew along the river but did not seem to be nesting in the area. On July 20, 1951, 105 miles southwest of Point Barrow, we observed Sabine's gulls, Arctic tern and several pairs of loons on one lake. On a return trip from Kaolak to Point Barrow by air

(July 27, 1951) we found Sabine's gulls generally distributed across the Coastal Plains. On an air trip from Point Barrow to Teshekpuk Lake on July 29, 1951, we noted two Sabine's gulls, one 9.7 miles southeast of Point Barrow and one 5.9 miles northwest of the central western edge of Smith Bay.

Three miles east of our camp on Barrier Lake (Aug. 3, 1951) a Sabine's gull had been eaten by a gyrfalcon. The gull was a bird of the year with the downy feathers extending beyond the ends of seven primary feathers. Three primary feathers were newly molted and of full length.

On an air flight (Aug. 4, 1951) from Teshekpuk Lake to Point Barrow we saw two Sabine's gulls 63 miles southwest of Point Barrow and two at 23 miles southwest of Point Barrow. At Point Barrow (Aug. 26, 1952), 250 Sabine's gulls were resting or flying in the area. On September 6 at 7½ miles south and 7 miles west of Point Barrow, Sabine's gulls constituted 60 per cent of the larger birds that were flying and feeding along the Arctic Ocean. The Arctic tern constituted 20 per cent, the kittiwake 5 per cent and the glaucous gulls 15 per cent of the population. An adult male shot here (Sept. 6) weighed 213 grams. Between Birnirk and Point Barrow (Sept. 11, 1952) we counted 17 Sabine's gulls feeding and resting along the shore of Elson Lagoon.

Sterna paradisaea Pontoppidan: Arctic tern.—Specimens, 11: 7½ mi. S and 7 mi. W Point Barrow, 156°49′15″, 71°16′52″, sea level, 2, Nos. 31315 and 31318, ad. male, Sept. 6, 1952; NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., 3, Nos. 30750-30752 including 2 ad. males and 1 ad. female, Aug. 1, 1951; Topagaruk River, 155°48′, 70″34′, 10 ft., 3, Nos. 30753, ad. female, July 7, 1951, and 30754, ad. male, July 9, 1951, and 30637, male, July 9, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 3, Nos. 30747-30749 including 2 ad. males, July 14, 18, 1951, and 1 ad. female, July 12, 1951.

Adult males and females prepared for specimens at Topagaruk (July 7, 9, 1951) showed signs of molting, especially in the primary wing feathers. Three adult males averaged 92(93-87) grams in weight (the largest male collected on the Arctic Slope was from Teshekpuk Lake on August 1, 1951, and weighed 106 grams). The testes of these males averaged 4.2(3-5) mm in length (in late autumn testes recede to approximately 1.0 mm in length). Two females from the same place and shot on July 7 and 12, weighed 99 and 100 grams. The average diameter of the largest ovum was 2.0 mm and the longest ovary was 6 mm.

At Kaolak River (July 12-18, 1951) an adult hunted day and night over shallow water on a sand bar approximately 500 yards from its nest. Water from lakes in an abandoned section of the river valley caused a creek to flow at night into the river. In the day ephemeral pools were formed because more water evaporated or sank into the sands. As pools were formed, small fish one inch in length were trapped. Before the pools disappeared, the tern captured all these fish. One of the terns that had been feeding on these fish flew out over the upland tundra approximately 500 feet from the river valley. This tern dove at us twice and then returned to the river valley and its nest some 800 feet away.

The nest of this bird was on one of three islands in a small lake. The nesting island was three square yards in area and had been built to a height of four feet above the level of the mainland by many years use of the island. The nest was within 30 feet of a nest of a red-throated loon, which was accepted in the territory of the tern without molestation.

Northeast of Teshekpuk Lake (July 29-Aug. 4, 1951) a pair of terns had young on a small island in a chain of lakes opening into the south end of Barrier Lake. The adults hunted small fish along the south end of Barrier Lake but especially in small lakes surrounding their nest. These birds seemed to be the only terns nesting on this large lake. As food was plentiful, available nesting sites may have governed the size of the tern population.

Six pairs of Arctic terns, constituting less than one per cent of the avian population in the area, were nesting on small islands of the larger lakes at Topagaruk in the period July 5-10, 1951. On July 8, one nest held both eggs and young; other nests held either eggs or young. These birds and the Sabine's gulls showed no hostility to one another. On July 9, three miles north of camp 13 terns were among sedges in standing water. They seemed to be nesting but we could not reach them.

On June 23, 1952, at a point 9/10 mile east and 8/10 mile north of Barrow Village, Arctic terns were in flocks; one of eight flew northeast across the tundra. At a point 105 miles northwest of Point Barrow on an air trip to Kaolak (July 20, 1951) we saw Arctic terns, Sabine's gulls, and several pairs of loons in the same lake. The trip from Point Barrow to Kaolak was characterized by relatively few large birds. On the return trip (July 27) on a straight line flight from Kaolak to Point Barrow, only two terns were seen, one 33 miles northeast of the junction of the Avalik and Kaolak rivers and another 9.7 miles beyond. On our return trip from Teshekpuk Lake to Point Barrow (Aug. 4, 1951) we saw only a single tern; it was 63 miles southeast of Point Barrow. At Gavia Lake (Aug. 21, 1952) there were three pairs of terns. At 8:00 A. M. three other pairs appeared and then left. No young were observed. At Point Barrow (Aug. 26, 1952) 130 terns fished or rested on the lee side of the peninsula. Arctic terns were the second most common bird flying and feeding along the shore line of the Arctic Ocean 10½ miles southeast of Point Barrow on September 6, 1952. Associated species were Sabine's gulls, kittiwakes and glaucous gulls.

Nyctea scandiaca (Linnaeus): Snowy owl.—Harmon Helmericks told us of seeing a snowy owl catch a brown lemming that was swimming in open water 30 nautical miles north of Thetis Island in April of 1946.

On a 1000 linear meter transect (1000 x 1) east of Barrier Lake we collected (Aug. 3, 1951) 19 pellets from the edge of the uplands and from prominent mounds on the lowlands. One pellet contained a complete radius-ulna of an Arctic fox and another a foot of a ptarmigan.

At Kaolak River (July 12, 1951) the only sign of owls was pellets on the upland tundra. They were covered with green algae and fungus several years old.

On an air flight from Point Barrow to Kaolak River (July 11, 1951) we saw one snowy owl on the Coastal Plain and on the return flight (July 19) two more; one was approximately 40 miles south of the Will Rogers monument and the other about one half way between the monument and Point Barrow. When flying from Teshekpuk Lake to Point Barrow (Aug. 4, 1951) we saw one snowy owl flying over the tundra.

Greater abundance was indicated by observations in 1952, a year in which brown lemming were at a high peak in their cyclic fluctuation: Entrails of a brown lemming were on top of a mound used by snowy owls as evidenced by the numerous fresh owl pellets, at the west side of Salt Water Lagoon on June 17; three snowy owls fed in the surrounding area (June 17-27); one owl seen at Driftwood on August 30-31; eight owls recorded on our two mile trip south of Barrow Village on September 6; four owls observed one half mile south of the Arctic Research Laboratory on September 7; three owls seen at Point Barrow on September 11.

Asio flammeus flammeus (Pontoppidan): Short-eared owl.—Specimen, 1: 2 mi. W Utukok River, 161°15′30″, 68°54′50″, 1275 ft., 1, No. 31319, ad. male, August 31, 1952.

A short-eared owl was seen at Chandler Lake on August 16, 1951. Another flew across the middle of Gavia Lake on August 22, 1952, hunted the south shore, caught two small rodents and pursued one Lapland longspur that escaped. From August 27 to 31, 1952, at Driftwood individual short-eared owls were noted daily. On August 31, a family group of five flew in close formation and fed in the low wet marsh in the valley adjacent to the river. An adult male from two miles west of Driftwood (Aug. 31, 1952) was 370 mm in length and weighed 417 grams.

Chordeiles minor minor (Forster): Common nighthawk.—Clifford Fiscus told us that a nighthawk was seen by an Eskimo in the summer of 1952 at Wainwright.

Tachycineta thalassina lepida Mearns: Violet-green swallow.—At 6:00 P. M. on August 17, 1951, at Chandler Lake, a northern violet-green swallow came to our camp, inspected us at a distance of four feet, fluttered over and around the tent for two minutes, then flew over the water, and continued south.

Corvus corax principalis Ridgway: Common raven.—Specimen, 1: Umiat, 152°08′, 69°22′, 337 ft., No. 31320, juv. female, August 19, 1952.

William Wyatte of Umiat told us that ravens were the only birds that remained at Umiat throughout the winter of 1951-52. He observed them flying when temperatures were so low that moisture from the ravens froze into floating ice crystals.

At Wahoo Lake (July 9, 1952) two ravens fed on a dead lake trout (18 inches in length) at the east end of the lake. The fish seemed to have died of malnutrition as it had an abnormally slender body and large head. No other carrion or dead fish was in the area. At 6:00 P. M. on August 8, 1952, in the main canyon 1/10 mile north of James Robert Lake, five ravens fed on remains of a dead caribou by extracting flesh from between the vertebrae; carnivorous mammals could not conveniently reach the flesh. A pigeon hawk harassed the ravens. Ravens were at Porcupine Lake, every day from July 13 to 18, 1952, mostly flying along the crest of high mountain ridges. One pair controlled a territory in the Canning River drainage east of Mount Annette and repelled an eagle on three occasions.

At the south end of Lake Peters (Aug. 10) a raven hunted low over the ground. Here, only occasionally were they seen so low in the valley. At Chandler Lake ravens were noted flying high along the crests of the mountains on August 11, 12, 13, and 25, 1951.

One juvenile female that was shot at Umiat on August 19, 1952, was 682 mm long and 1360 grams in weight. Between August 30 and September 4, 1951, ravens were noted at Umiat every day; the largest group was six. Most of the time they fed at the refuse pile near camp.

On our first day at Gavia Lake (Aug. 21, 1952) a pair of ravens arrived from the west and calling continually circumnavigated the shore line. They left in the same direction from whence they came.

Clifford Fiscus told us that in the summer of 1952, ravens were seen along the Arctic Coast between Pitt Point and Point Barrow. The largest congregation was at the mouth of the Colville River. Ravens were noted on August 27 and 28, 1952, at Driftwood.

Turdus migratorius migratorius Linnaeus: Robin.—From the tops of alder trees at the mouth of Bearpaw Creek on June 27, 1952, three robins sang more frequently in the evening between 6:00 P. M. and 11:00 P. M. than at any other period of the 24 hours of continuous daylight.

At Wahoo Lake on July 3, 1952, a nest held four eggs, on July 6 two eggs and two young, and on July 10 one egg and three young. On July 12 the single egg was determined to be infertile. In the canyon south of Wahoo on July 6 two adults and a single young bird were feeding 50 feet from a recently abandoned nest that was superimposed upon an old nest of a previous year. Other robin nests in high willows in the bottom of this canyon were spaced approximately ⅕ of a mile apart. Occasionally robins foraged on the open tundra beyond willow-lined creeks. As compared with robins in the temperate regions, those in the Arctic Life-zone were notably less "fearless"; they came to within three feet of the nest when nestlings were being inspected by an observer. The robins at Wahoo Lake on July 3-12, 1952, generally sang at about 10:00 P. M., a time equivalent to twilight in temperate regions to the south.

Hylocichla minima minima (Lafresnaye): Gray-cheeked thrush.—Specimens, 2; Wahoo Lake, 146°58′, 69°08′, 2350 ft., 1, No. 31321, ad. female, July 11, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 1, No. 30755, juv. male, August 23, 1951.

On June 27, 1952, we frequently heard thrushes singing on the side of the valley north of Umiat. Large alder, birch and willow gave adequate protection to these birds.

At Wahoo Lake (July 3-12, 1952) thrushes were seen every day along willow-lined creeks. An adult female on July 11, was 191 mm long and weighed 34 grams. A male from Chandler Lake on August 23, 1951, was 186 mm long and weighed 34 grams. It was caught in a mouse trap on an alluvial outwash at the mouth of a canyon in a willow community in which some willows were as high as nine feet. Fifteen tree sparrows, two white-crowned sparrows, one northern shrike, two wheatears and a few redpolls were noted there.

Oenanthe oenanthe oenanthe (Linnaeus): Wheatear. — Specimens 2: Mount Mary, S end Lake Peters 145°10′02″, 69°20′30″, 2920 ft., 1, No. 31322, juv. female, August 1, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 1, No. 30756, ad. male, August 12, 1951.

On the top of Mount Annette (July 17, 1952), which is the highest peak in the valley and the center of several drainage systems, the insects had collected in unusual numbers. There, an adult wheatear was feeding insects to her young, which were three fourths the size of the parent.

From records kept of trap catches at Lake Peters (July 31-Aug. 15, 1952) the wheatears were always caught in those areas that supported the greatest number of red-backed voles (*Clethrionomys rutilus*). On August 10, among rocks at the base of moraines, the wheatear was the second most common species. On August 15, after snow had fallen on the mountain and in the valley and the skies there were cloudy, wheatears moved onto the alluvium but always within at least 150 feet of moraines to which the birds retreated when alarmed. An adult female, shot on August 1, on the lower slopes of Mount Mary at the south end of Lake Peters, was 158 mm long and weighed 26 grams.

At Chandler Lake (Aug. 9-25, 1951) the wheatear was characteristically a bird of the rock fields and rockslides and in many places was the only bird present. It did not inhabit the glaciated canyons leading west from Chandler Lake, except at their mouths. From August 10-19, wheatears decreased in numbers. On August 25 the two remaining birds noted were among willows and rock ridges. Three adult males, shot on August 14, averaged 24(23-26) grams in weight and their testes averaged 1.2(1.0-1.5) mm long.

Luscinia svecica svecica (Linnaeus): Bluethroat.—Specimens, 7: Gavia Lake, 150°00′, 69°35′, 460 ft., 2, Nos. 31323 and 31328, males August 22, 23, 1952; 9/10 mi. W and 9/10 mi. N Umiat, 152°10′58″, 69°22′53″, 380 ft., 1, No. 31324, ad. female, June 30, 1952; Driftwood, Utukok River, 161°12′10″, 68° 53′47″, 1200 ft., 3 (skins) Nos. 31326 and 32620, ad. females and 31327, ad. male ?, August 29, 1952, and 1, No. 31325, ad. female, August 28, 1952.

The average length and weight of six adult males and adult females from Gavia Lake and Driftwood (Aug. 23-29, 1952) are, respectively, as follows: 153(148-165) mm and 19(18-21) grams. One female from Umiat shot on June 30, 1952, weighed 22 grams. The ovary was 5 mm long and the largest ovum was 1 mm in diameter.

At Umiat (June 30, 1952) a bluethroat was captured in one of 200 traps placed around the edge of a small lake. The trap that held the bird was in a soil fracture 15 centimeters in depth in an area that supported alder, willow, birch and ericaceous shrubs. At Driftwood, a bluethroat was caught on August 28, 1952, in a trap set among willows.

Phylloscopus borealis kennicotti (Baird): Arctic warbler.—On the north side of the valley at Umiat on June 27, 1952, willow warblers sang loudly and continually in accompaniment with white-crowned sparrows, tree sparrows, gray-cheeked thrushes and bluethroats.

Motacilla flava tschutschensis Gmelin: Yellow-wagtail. — Specimens, 2: Kaolak, 160°14′51″, 69°56′00″, 178 ft., 1, No. 30757, ad. female, July 27, 1951; Umiat, 152°09′30″, 67°22′08″, 352 ft., 1, No. 31329, ad. female, June 26, 1952.

At Umiat on June 25, 1952, a nest of the wagtail was on the side of a mound of earth three feet high. The nest, 130 mm in diameter and 14 grams in weight, was completely protected overhead. The lower half of the cup, 59 mm in diameter and 35 mm in depth, was lined (3 mm in thickness) with hair of caribou and brown lemming; the upper half was of feathers. Beneath the lining of the cup was 38 mm of moss. The outer nest, 33 mm in thickness, was, of coarse stems of grasses and other material. The nest was not so carefully constructed nor so well insulated as nests of tree sparrows, longspurs and snow buntings; it lacked the fine yellow grasses and symmetrical lamination of the materials and had more large chunks of material thus producing an irregular shape. Both male and female remained in the air directly overhead for 15 minutes as we examined the nest and then followed us for 100 yards as we left the area. An adult male shot on June 26, was incubating four eggs. He was 165 mm in length and weighed 19 grams.

On July 27, 1951, seven days after our arrival at Kaolak, a male and female were seen for the first time. They flew back and forth overhead and called as if defending a territory but probably were not as we had been through this same area many times without either seeing or hearing these birds; also the female's ovary was undeveloped.

Anthus spinoletta rubescens (Tunstall): Water pipit.—Specimens, 3: Mount Mary, S end Lake Peters, 145°10′02″, 69°20′30″, 2920 ft., 1, No. 31330, juv. female, August 3, 1952; Wahoo Lake, 146°58′, 69°08′, 2350 ft., 2, Nos. 31331, female, July 7, 1952 and 31332, ad. male, July 8, 1952.

On July 8, 1952, approximately two miles south of Wahoo Lake on a high divide an adult was feeding a young bird 114 millimeters in total length and just able feebly to fly. On July 17, 1952, an adult female was feeding young on top of Mount Annette south of Porcupine Lake. Numerous insects had converged there—the highest point in the range of mountains. At Porcupine Lake, we observed water pipits on each of the five days July 13 to 18, 1952.

At Lake Peters there was a definite increase in numbers and in movement of water pipits with the approach of winter. This increase was correlated with a decrease in temperature and an increase in rain and snow. The many individuals and family groups, which, prior to our arrival, were generally distributed on the higher slopes and in the canyons of the Brooks Range, left the lower snow-covered slopes and congregated on the lake shore. On July 19, 1952, at the north end of Lake Peters, for example, we did not see water pipits in their usual haunts. On July 31 a single individual was noted at the south end of Lake Peters and on August 3, a single family appeared. On August 10, the water pipits were the most common bird at the edge of the lake, five or six usually being seen in a half hour trip. One flock of 14 bathed in shallow pools along the edge of the lake. These birds in the last few days had been congregating in small and large groups. On August 13, on a trip along the west shore line from the south end to the north end of the lake, the only birds seen were water pipits and these were in great numbers. On the morning of August 15, there was a dramatic increase in the number of pipits along the edge of the lake. Twenty of these birds fed 10 feet in front of our tent and others perched on its top. A juvenile shot on August 3 on Mount Mary was approximately the size of the adults, being 162 mm in length and 17 grams in weight.

At Chandler Lake (Aug. 12, 1951) pipits fed along the sandy edge of the lake and among short sedges. These birds also fed on scraps of food at the entrance of our tent door. From August 10 to 25, water pipits were more commonly found in the east-west canyons whereas other kinds of small birds were almost wholly confined to the north-south valley and were of only accidental occurrence in areas inhabited by water pipits.

Lanius excubitor invictus Grinnell: Northern shrike.—A bird was noted on August 23 and 25, 1951, in an extensive stand of willows at Chandler Lake.

This bird was one of a few birds that had not yet departed from the area with the advent of winter.

Acanthis flammea holboellii (Brehm): Common redpoll.—Specimens, 12: Topagaruk River, 155°48′, 70°34′, 10 ft., 1, No. 30767, ad. male, July 9, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 5, Nos. 30762-30766 including 4 ad. males and 1 ad. male (?), July 12, 14, 16-18, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., 4, Nos. 30758-30761 including 1 ad. male, 2 ad. females and 1 ad. of unknown sex, July 21, 23, 1951; Umiat, 152°09′30″, 69°22′08″, 352 ft., 1, No. 31333 ad. female, June 26, 1952; Wahoo Lake, 146°58′, 69°08′, 2350 ft., 1, No. 31334, ad. male, July 11, 1952.

At Umiat on June 26, 1952, a nest of five eggs (embryos with natal down) was located in a patch of willows that covered approximately two square meters. As these willows had not as yet acquired leaves, the nest was clearly visible. It was 300 millimeters from the ground and so compactly made as to support its own weight. The outer structure was of various plant fibers and other stems of willows. The cup had an inwardly reflected rim, was made of stems of cotton-grass, and was well insulated with 15 mm of down feathers. The measurements of this circular nest were: entire nest, 78 mm in diameter and 50 mm in depth: cup, 42 mm in diameter and 35 mm in depth; weight, 9 grams. Another nest of three eggs from the same area was in a dwarf willow 350 mm from the ground. The leaves of the willow were undeveloped. A third nest of six young approximately three days old, was two feet up in a dwarf willow having no leaves. The young birds in the nest were three days old. One female 123 mm in length shot on June 26 had ova up to two mm in diameter. At Umiat (June 28, 1952) a nest of three young and two eggs was found and on June 30 another nest with one fresh egg.

At Wahoo Lake (July 3-12, 1952) the redpolls were observed every day but we considered them relatively uncommon there.

At Topagaruk (July 5-10, 1951) redpolls were among willows growing on the sides of a creek channel ten feet below the level of the tundra. This creek had overflowed in early spring covering the willows. One of the birds approached us to within five feet and after making a close inspection returned to the willows.

Upon our arrival at Kaolak River (July 12, 1951) most of the redpolls were living among willows and only occasionally flew overhead. On July 15, they were flying in small groups about 100 feet above the ground and were calling continually. On July 15, on a four hour field trip, we counted 28 birds. The young birds on this date could fly well.

At Porcupine Lake these birds were uncommon but a few were seen (July 17, 1952) flying south across divides in the higher mountains.

At Kaolak (July 20-27, 1951) redpolls were associated with willows along creeks that had cut channels 20 feet deep. In late July the flowing water was six feet wide and from a few inches to three or four feet deep. The first erosional bench supported grasses and sedges and the slopes were covered with willows from a few inches to seven feet high. These willows afforded nesting sites for redpolls. In a two-mile stretch along this creek, which drained east into the Kaolak River (July 21), there were approximately 200 redpolls, 100 Lapland longspurs, 80 savannah sparrows, six willow ptarmigans, six pintail ducks and several other smaller unidentified birds. On this same date when I walked four miles on the open tundra, there were, of the smaller birds, only six redpolls, 20 Lapland longspurs and 13 savannah sparrows. In one interval of ⅓ of a mile, I did not see a single individual of any of these three species. In the two miles of creek bottom that I examined, there were several nests that had been used that spring, several that had been used the year before, and one that held four eggs containing embryos nine millimeters in length (no feathers or bone development). Most of the nests were approximately three feet above ground in willows near the creek. The nest of four eggs was three feet above the ground, three feet from the edge of the willows bordering the creek, and 10 feet from the creek proper. The nest was 10 cm in diameter and 55 mm in height. The cup was 5 cm in diameter at the upper rim, six cm in width and 35 mm in depth. The outer base and side were constructed of dry willow sticks, twigs and grass stems; the main body of the nest was fine grass stems, rootlets and a few mosses. This lining was a layer 18 mm thick of white feathers. The weight of this nest was 12 grams. The four eggs measured 19.2 x 12.9, 18.3 x 12.5, 18.3 x 12.8, 17.7 x 12.9. This nest of four eggs was either a second nesting or an interrupted or exceptionally late first nesting of redpoll on the Arctic Slope. Two abandoned nests 200 feet apart were in willows along the edge of an oxbow lake at Gavia Lake (August 23, 1952).

On August 10, 1952, at the south end of Lake Peters, there was only a slight increase in the number of redpolls over the previous week. At Chandler Lake (Aug. 25, 1951) a few redpolls were among willows, this was the first time in 15 days that we had noted these birds. One redpoll was taken in a trap at Umiat on August 30, 1951.

The testes of six adult males (average 14(13-15) grams in body weight and that were shot at several localities on the Arctic Slope from July 9 to July 28, 1951) averaged five mm in length.

Spinus pinus pinus (Wilson): Pine siskin.—An adult male, which weighed 12 grams, was caught in a trap at Chandler Lake on August 14, 1951. The testes were two mm long.

Passerculus sandwichensis anthinus Bonaparte: Savannah sparrow.—Specimens, 19: Kaolak, 160°14′51″, 69°56′00″, 178 ft., 12, Nos. 30770-30781 including 3 ad. males, 3 juv. males, 4 ad. females, 1 juv. female and 1 ad. female (?), July 21-23, 25, 26, 1951; Gavia Lake, 150°00′, 69°35′, 460 ft., 1, No. 31336, juv. male, August 22, 1952; Wahoo Lake, 146°58′, 69°08′, 2350 ft., 1, No. 31337, ad. male, July 5, 1952; Porcupine Lake, 146°29′50″, 68°51′57″, 3140 ft., 1, No. 31339, ad. female, July 13, 1952; Driftwood, Utukok River, 161°12′10″, 68°53′47″, 1200 ft., 1 (skin) No. 31338, male and 1 No. 31335, ad. female, August 29, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 2 Nos. 30768-30769, 1 ad. male and 1 juv. male, August 10, 15, 1951.

Savannah sparrows were caught in traps in the following communities: damp meadow of sedges, Chandler Lake, August 10, 1951; among sedges bordering a lake, Wahoo Lake, July 5, 1952; damp to wet meadow of sedges, grasses, and hummocks of cotton-grass, Porcupine Lake, July 14, 1952; along the edge of a deeply incised stream running through a marsh, Porcupine Lake, July 16, 1952.

At Kaolak (July 21, 1951) on a windy day the greater number of savannah sparrows were in protected valleys of willows along the creeks and not on the open tundra where they are normally found. In a two mile course along one creek there were 80 birds, whereas on the open tundra there were, in four miles, only 13 birds.

Weights of 10 males and 10 females, shot in the period July 14-August 29, 1951, at several localities on the Arctic Slope were: male 20(17-24), female 18(16-20) grams. In an adult male, shot on July 22 at Kaolak, the testes were two mm long but in other males, shot in the period July 14-August 29, the testes averaged 1.2 mm. The ovaries of adult females for this same period also had receded to normal non-breeding size. Juveniles on July 13 at Porcupine Lake averaged 20 grams in weight; the shortest was 125 mm in total length and the largest 140 mm. Adults in this same period averaged 144 mm in total length. Two adult males collected on July 22 and 24, 1951, at Kaolak, were molting.

Spizella arborea ochracea Brewster: Tree sparrow.—Specimens, 10: Gavia Lake, N White Hills, 150°00′, 69°35′, 460 ft., 1, No. 31340, juv. male, August 22, 1952; 9/10 mi. N and 9/10 mi. W Umiat, 152°10′58″, 69°22′53″, 380 ft., 1, No. 31347, ad. female, July 1, 1952; Umiat, 152°09′30″, 69°22′08″, 352 ft., 1, No. 31341, ad. male, June 26, 1952; Wahoo Lake, 146°58′, 69°08′, 2350 ft., Nos. 31342-31343, ad. males, July 6, 8, 1952; Driftwood, Utukok River, 161°12′10″, 68°53′47″, 1200 ft., 2 (skins) Nos. 31345, ad. male, August 29, 1952, and 31346, ad. female, August 28, 1952, and 1, No. 31344, ad. male, August 28, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 2, Nos. 30783, juv. male, 30784, a juv. of unknown sex, August 19, 1951.

Four adult males shot in the period July 1-15, at Umiat, Wahoo and Porcupine lakes averaged 158(155-165) mm in total length and 18(16-18) grams in weight whereas 12 adult males (Aug. 14-31) from Chandler Lake, Umiat, Gavia Lake and Driftwood averaged 161(156-165) mm in length and 19(16-21) grams in weight. A male (June 26) from Umiat was 160 mm long, weighed 15 grams, and had testes 4 mm long. Males from Wahoo Lake (July 6 and 8) had testes 9 and 5 mm long. Males (August 19) from Chandler Lake were molting on the entire body.

On June 24, 1952, at Umiat, we examined three nests. One of the three contained incubated eggs; skeletal elements were present in the embryos. This nest, 150 mm in diameter and 52 mm in depth, was on the side of a mound three feet high covered with grass. The cup was 55 mm in diameter. The lining, 14 mm thick, was ptarmigan feathers averaging one inch long mixed with successive layers of stems of fine grass. The cup weighed four grams and rested directly on the ground. The outer part of the nest was coarse stems of a grass and was 30 mm thick. The edge and upper side, away from the mound, had a 40-millimeter thickness of mosses and lichens that may have served primarily as camouflage rather than as insulation. The nest, minus the lining weighed nine grams. The second nest held four eggs containing embryos. The top was flush with the surface of the ground on a slightly elevated bench on a hillside supporting *Ledum, Vaccinium, Alnus,* mosses and lichens. The greatest width of the nest was 120 mm; the lining, 11-millimeters thick, was of ptarmigan feathers succeeded by 13 mm of alternating layers of new dry grass stems and ptarmigan feathers. The down-slope side of the nest was protected by 29 mm of sphagnum, old grass stems and other dry plant material. The third nest of four eggs was among grasses at the base of a willow. The new leaves on this willow were just visible and the catkins had attained full growth.

The earliest date that juvenal tree sparrows were noted in the field was on July 10, 1952, at Wahoo Lake. One juvenile shot on this date was 85 mm long and could not fly. The parent bird was still attending the young bird.

Tree sparrows on the Arctic Slope usually live among high dwarf willows at the mouths of canyons. At Porcupine Lake (July 13-18, 1952) however, they inhabited marshes of sedges, grasses and hummocks of cotton-grass. At night they roosted in depressions in the ground or between hummocks of sedges, where, without overhead protections they endured temperatures of as low as 34 degrees Fahrenheit.

In one mile of a glaciated canyon southwest of the south end of Chandler Lake (Aug. 19, 1951) tree sparrows were the commonest species but there were few birds of any kind there. This canyon extended in an east-west direction and was bordered by high mountains, the sun being excluded in early morning and late afternoon. In the valley of Chandler Lake, on the same day, the tree sparrows were numerous especially among willows on the side of the valley. On this date there was an abrupt increase in numbers of tree sparrows; the number of Lapland longspurs and wheatears was less than a week before. On August 22, we did not see tree sparrows at Chandler Lake whereas three days earlier there were hundreds in the area. On August 23 only 15 were noted and these were in willows. On August 25, only a single bird was noted.

At Umiat (Aug. 30, 1951) a few tree sparrows were present. In this area (Sept. 1) the birches were turning a brilliant red, even more brilliant than on the previous day. The large alders were nearly all yellow. The season was not so far advanced here, however, as at Chandler Lake on August 25. At Driftwood tree sparrows were noted from August 27 to 31 inclusive. On August 28 a flock of 12 was observed.

Zonotrichia leucophrys gambelii (Nuttall): White-crowned sparrow.—Specimens, 3: Mount Mary, S Lake Peters, 145°10′02″, 68°20′30″, 2920 ft., 1, No. 31348, juv. female, August 3, 1952; Driftwood, Utukok, 161°12′10″, 68°53′47″, 1200 ft., 1 (skin) No. 31349, ad. male, August 29, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 1, No. 30786, an ad. of unknown sex, August 19, 1951.

On the north side of the valley at Umiat, the white-crowned sparrows were calling (June 27, 1952) throughout the day. At Wahoo Lake (July 3-11, 1952) singing birds were frequently heard on south-facing slopes of the valley. At Lake Peters (Aug. 3, 1952) one bird was at the base of a moraine some distance from willows or high vegetation. Only two birds were seen at Chandler Lake (Aug. 19 and 25, 1952); they were feeding in a dense growth of willows. The juvenal female shot on August 3, 1952, at Mount Mary was 180 mm long and weighed 26 grams.

Zonotrichia atricapilla (Gmelin): Golden-crowned sparrow.—Specimen, 1: Chandler Lake, 152°45′, 68°12′, 2900 ft., No. 30787, ad. male, August 19, 1951.

Passerella iliaca zaboria Oberholser: Fox sparrow.—Specimen, 1: Driftwood, Utukok River, 161°12′10″, 68°53′47″, 1200 ft., No. 31350 (skin), male, August 29, 1952.

At 1⁄10 mile west and 9⁄10 mile east of Umiat (June 30, 1952) a nest the top of which was flush with the ground in a clearing among willows and alders, both bare of leaves, had four young approximately five days old. At Driftwood (Aug. 29, 1952) a male was caught in a mouse trap in the same area where a male was singing on the previous day. At the time the male was trapped a female sat on low vegetation only a few feet from the trap that held the dead bird.

Calcarius lapponicus alascensis Ridgway: Lapland longspur.—Specimens, 75: NE Teshekpuk Lake, 153°05′40″, 70°39′40″, 8 ft., 22, Nos. 30827-30848 including 10 ad. males, 9 juv. males, 2 ad. females and 1 juv. female, July 29, 30, August 1, 3, 1951; Topagaruk River, 155°48′, 70°34′, 10 ft., 13, Nos. 30849-30861 including 9 ad. males and 4 ad. females, July 6, 8, 10, 1951; Kaolak River, 159°47′40″, 70°11′15″, 30 ft., 18, Nos. 30809-30826 including 2 ad. males, 10 juv. males, 3 ad. females and 3 juv. females, July 12, 14, 17, 1951; Kaolak, 160°14′51″, 69°56′00″, 178 ft., 13, Nos. 30796-30808 including 4 ad. males, 4 juv. males, 5 juv. females, July 20-27, 1951; Gavia Lake, 150°00′, 69°35′, 460 ft., 1, No. 31351, female, August 22, 1952; Umiat, 152°09′30″, 69°22′08″, 352 ft., 1, No. 31352, female, June 26, 1952; Chandler Lake, 152°45′, 68°12′, 2900 ft., 7, Nos. 30789-30795 including 1 ad. male, 1 juv. male, 1 ad. female, 4 juv. females, August 11, 12, 16, 18, 23, 1951.

The Lapland longspur and snow bunting were two of the early arrivals on the Arctic Slope of northern Alaska. Robert McKinley told us that this species of longspur arrived at Barrow Village shortly after April 20, 1952. On our arrival at Point Barrow on June 14, 1952, longspurs already were established on territories, and many of the birds had full complements of fresh eggs, although snow still covered the lakes and all but a few mounds and high points of the tundra.

On June 17, 1952, on the west side of Salt Water Lagoon, in an area of approximately six acres of raised polygons we located eight nests of the Lapland longspur. The first contained five fresh eggs, and its top was flush with the bare ground in an old excavation made by brown lemmings between three bunches of cotton-grass. Fecal pellets of the brown lemming were beneath the nest. The bulk of the nest was soiled grasses which insulated the bottom and sides of the nest from the damp soil. This supporting bulk was lined first with stems of new yellow grass, and then with white down feathers of the snowy owl. The female repeatedly repelled the male from the immediate vicinity of the nest. After observing the nest for a few minutes I moved it one foot. The female returned three times to the original site of the nest, ignoring the nest nearby. On the fourth trip, six minutes after the original nest was taken, she returned with feathers in her bill and started to line the original depression.

The second nest, superimposed on a nest of the previous year, held six fresh eggs and was under an overhanging piece of tundra sod. The cup was entirely beneath the sod but the outer rim of the nest was exposed. The nest faced northwest and was 100 centimeters above the general level of the tundra. Measurements, in millimeters, of this nest were: height, 52; width, 120; inside diameter of cup, 50; depth of cup, 30; width of layer of fine grasses and feathers of cup, 16. In cross section successive layers of nest material from outside in were as follows: mosses; old, dry, brownish-gray grasses; new, fine, loosely arranged, yellow grasses; down feathers of the snowy owl. The first two layers were on only one side and did not extend under the cup of the nest. The cup was lined with 12 down feathers of the snowy owl.

The third nest, containing six fresh eggs, was at the edge of a clump of cotton-grass and was exposed from directly above. The lining of the cup of white feathers and dry lichens was against the soil. Two layers of dry brownish-gray grasses and dry mosses were outward extensions from the cup.

The greater part of the third nest was stems of the grass *Dupontia fischeri;* newer yellow stems were near the cup and the older stems were toward the periphery. The measurements (in millimeters) of this nest were: height, 60; width, 210; width of cup, 50; depth of cup, 40.

A fourth nest of three fresh eggs held four eggs the following day. A fifth nest of six fresh eggs was only 10 centimeters from a well-used trail of a brown lemming and within ⅓ of a meter from the underground nest of the lemming. This longspur nest, among polygons of low hummocks, was bordered by mosses and grasses nine inches high. The sixth nest held five fresh eggs. Its top was flush with the ground and the nest was protected by an overhead canopy of *Dupontia fischeri.* A seventh nest, containing six fresh eggs, was among pieces of tundra displaced by a vehicle. Only the outer edge of this nest was exposed from above. The cup was lined with white feathers and with the hair of *Rangifer.* On June 20, an eighth nest of five fresh eggs was located near the above. The nest was ⅓ concealed under overhead protection.

At a point 1⅗ miles south and ⅗ of a mile east of Barrow Village (June 20, 1952) we examined a ninth nest, containing six fresh eggs, among raised polygons. It was circular and the cup was centrally placed. The entire nest weighed 14 grams; the inner cup of fine stems of grass and white feathers weighed two grams. The nest was 118 mm wide; the cup was 56 mm wide and 38 mm deep. The outer structure of last year's nest, mosses and larger gray stems of grass, was 30 mm wide. Enroute to this locality from Barrow Village we saw only two longspurs (2:00 P. M.) and only three on the return trip.

At a place 9/10 mile east and 8/10 mile north of Barrow Village (June 23, 1952) a tenth nest, containing five fresh eggs, was noted in a lemming runway that had been enlarged from a soil fracture. The top of the nest was flush with the surface of the ground and there was no overhead protection. This nest had the least nesting material of any nest of this species examined to date; there was no nesting material of any kind on the sides adjoining the walls of the fracture. At Umiat (June 26, 1952) an eleventh nest, containing six eggs, was so placed that its top was flush with the surface of a raised polygon, and closely resembled those at Point Barrow except that the cup was lined with brown and white feathers of the willow ptarmigan. Additional data are as follows: weight of entire nest, 20 grams; weight of inner cup, 7 grams; diameter of cup, 65 mm; depth of cup, 30 mm; width of entire nest, 100 mm. As was usual with other nests of this species, the outer edge of one side was covered with moss.

In the period July 13-August 15, from several localities on the Arctic Slope, Lapland longspurs were caught in traps (20 feet apart) set in linear lines among sedges. The average distance between traps catching longspurs was 1400 feet. Other Lapland longspurs observed in the same period at these same localities averaged one per 400 feet of walking on my part. The greatest number of longspurs trapped was at Kaolak on July 24, 1951; 100 traps yielded 6 longspurs. The greatest number observed—one per 100 feet—was at Topagaruk on July 5, 1951. Although the longspur on the Arctic Slope, is the most common bird, it is absent from some areas there. On each of two trips (July 29-30) across one mile of upland plateau between Barrier Lake and Teshekpuk Lake, we did not see longspurs. This plateau is a travel lane maintained by caribou.

Juveniles were first trapped on July 5, 1951, at Topagaruk; others were observed on this date but they could not fly. The first juvenile noted in flight was on July 9, also at Topagaruk. The increase of juveniles there caused the longspur to be the most common bird in the field (50 per cent in abundance). On July 15 at Kaolak River, most of the longspurs noted were juveniles, but they were able to fly well. The adult males and females, which were molting at this time, were more secretive in their movements than longspurs at Topagaruk on July 5. Adult males were molting as early as July 2 at Kaolak. On July 25 at Kaolak longspurs were mainly in groups of five or six; others were in groups of 18 or more. As late as August 21 (Gavia Lake) longspurs were still in family groups or occurred as singles.

At Chandler Lake, the decrease in numbers of Lapland longspurs was synchronized with autumnal changes in weather. On August 15, 1951, the longspurs were numerous; 40 or 50 individuals were seen in the course of an hour's walk. On August 19 there was a noticeable decrease in numbers of individuals and by August 22, only three were seen. In this period of decreasing numbers, they were more numerous and active in the morning than in the evening or in inclement weather. The behavior pattern of leaving the ground with an audible commotion and flapping of wings on the vegetation also was characteristic of this period of decreasing numbers of the longspur population. At ½ mile south of the Arctic Research Laboratory (Sept. 7, 1952) only a single longspur was noted.

The short-eared owl and especially the pigeon hawk consistently preyed on longspurs.

Only one longspur (an adult female No. 30854) in 75 specimens examined had the bone of the skull damaged by parasites.

Adult males are larger than adult females (July). In the breeding season adult females average 3 grams lighter than males. In the latter part of summer, however, females "catch up" in weight with the males. As early as the middle of July, juveniles are nearly as large as adults in cranial measurements. The increase in weight in juveniles was from 21.5(18-25) in ten juvenal males shot in the period July 12-16, at Kaolak River to 25.2(22-27) grams in nine juvenal males shot in the period July 29-August 2 at Teshekpuk Lake.

The testes of adults gradually decrease in size from July to August; their average length was 7.7(4.0-12.0) mm in nine adult males shot in the period July 6-10 at Topagaruk but only 2.2(1.5-3.0) in six adult males shot in the period July 12-26, at Kaolak and Kaolak River. By August 1, at Teshekpuk Lake the testes of nine adult males averaged 1.4(1.0-1.5) in total length, which is only slightly larger than the average size of the testes 1.2(1.0-2.0) of nine juveniles shot in the period July 29-Aug. 2, at Teshekpuk Lake.

Calcarius pictus (Swainson): Smith's longspur. — Specimens, 2: Wahoo Lake, 146°58′, 69°08′, 2350 ft., No. 31353, ad. male, July 9 and No. 31354, ad. female, July 7, 1952.

On July 7, 1952, at Wahoo Lake, a single longspur was trapped in one of 200 traps set for small mammals. On July 9, a line of 120 traps set in a community of cotton-grass, other sedges, grasses and dwarf willow also yielded one longspur—an adult male 172 mm long that weighed 28 grams. Smith's longspurs were uncommon at Wahoo Lake from July 3 to July 11, and when seen were associated with open tundra supporting cotton-grass, generally on flat areas adjacent to the lake. Singing from the air was heard on several occasions. On the alluvial outwash, between Lake Peters and Lake Schrader, two Smith's longspurs were recorded on July 24, 1952, and flocks of 11-16-18-20 were seen there in the damp meadows on August 13, 1952. Those seen on the latter date had moved into the area since July 23, when we first arrived.

Plectrophenax nivalis nivalis (Linnaeus): Snow bunting.—Specimens, 6: Topagaruk, 155°48′, 70°34′, 10 ft., 5, Nos. 30862-30866 including 4 ad. males and 1 ad. female, July 6, 7, 9, 10, 1951; Mount Mary, S end Lake Peters, 145°10′02″, 69°20′30″, 2920 ft., 1, No. 31355, August 1, 1952.

Robert McKinley reported to us that snow buntings were at Barrow Village at least as early as April 20, 1952, when snow covered most of the ground. On June 14, 1952, at Birnirk mounds when snow still covered most of the ground, snow buntings were already established on territories.

At Point Barrow (June 21, 1952), the most northerly extension of land on the Arctic Slope of northern Alaska, five pairs of snow bunting were nesting in abandoned subterranean Eskimo houses. The houses were in different stages of deterioration from one almost usable by man to one that was no more than a flattened mound. Sides of some houses were exposed by the sea cliff that was advancing inland. Logs and skulls of baleen whales had been set on end for walls, and mandibles and ribs of whales had been used as rafters. This framework had been covered with tundra sod. Most of the nests were between the roof support and the upper ends of the whale skulls. Each nest contained five fresh eggs and was completely protected from rain, sun and wind. One nest weighed 24 grams and measured (in millimeters) 155 wide, 68 high, 38 in depth of cup, 70 in width of cup, and was in the brain cavity of the cranium. Another nest on top of a skull in the interior room, weighed 24 grams. This nest was built upon material of a nest of the previous year. The old material weighed four grams and the new inner mass weighed 20 grams. The new nest consisted of successive layers of new yellow grass stems and feathers. The lining of the cup had feathers in the 20 mm-thick layer of fine hairlike plant fibers. The feathers were from birds larger than the bunting. The nest was well insulated in comparison with those of the Lapland longspur, but like most of those had the cup offset toward the inner side of the nest, and more nest material of large size outward toward the entrance, then elsewhere. In the same area, especially in grass on and around low mounds, there were approximately 50 brown lemmings (18 lemming nests examined), many of which used the mounds inhabited by the bunting. On August 26, in the same area at Point Barrow, we noted 28 birds feeding and resting but on September 11 found none there.

A nest of five young (July 4, 1951) at a place ⅕ mile south of the Arctic Research Laboratory was under an overhanging ledge of an unused burrow of a brown lemming. The burrow had been excavated by lemmings on a mound of earth thrown up by a bulldozer. An adult female snow bunting was carrying insects to the nest and fecal pellets away from it. Another nest of five young (July 4) was in a fifty gallon oil drum. An adult female gained entrance to the nest through a small hole on the side of the container, the only hole present. Other nests on this date were examined that contained both eggs and young, or eggs, or young. Most of these nests were in holes in the ground or under the protection of overhanging ledges of earth. On July 4, snow buntings were in their black and white plumage, but on July 27, were in brown-white plumage.

At Topagaruk (July 5, 1951) a nest containing young birds fully feathered was noted five feet above the ground in a horizontal pipe six inches in diameter. One dead bird, two to three days old, was in the water and mud at the base of the stack of pipes. Other young birds from other family groups had short tails and were capable of feeble flight. Adults were seen only in the immediate vicinity of the camp.

The average weight of four adult males shot in the period July 6-10, 1951, was 36 grams. The average length of their testes was 9.2(7.0-11.0) mm.

At Kaolak (July 21-27, 1951) we did not see the snow bunting. The camp, however, was built the previous winter and was inhabited (July 10) for the first time in summer. The birds were at Topagaruk, our collecting station next nearest to the eastward in the same general type of environment and we assumed that eventually the birds would become established at Kaolak.

A juvenal female shot on August 1, 1952, at Mount Mary was 183 mm long and weighed 34 grams.

Transmitted November 14, 1957.

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19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-337. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
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31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
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4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
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13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.
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10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
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MUSEUM OF NATURAL HISTORY

Vol. 10, No. 6, pp. 213-552, 34 plates, 8 figs., 35 tables in text
November 7, 1958

The Wood Rats of Colorado: Distribution and Ecology

BY

ROBERT B. FINLEY, JR.

UNIVERSITY OF KANSAS
LAWRENCE
1958

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

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Published November 7, 1958

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1958

26-8049

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CONTENTS

INTRODUCTION

Since the earliest beginnings of Natural History, one of the most fruitful approaches to an understanding of animals and the biological principles that account for their existence has been study of their distribution. In early years the interests of naturalists were directed mainly toward the description and comparison of faunas from all parts of the world. The wealth of facts thus accumulated has led (one might even say, driven) zoologists to a better understanding of evolution, phylogeny, adaptation and ecological relationships. Since about 1900 much progress has been made in detailed studies of animal life histories, behavior, and population dynamics. Most of these studies, of necessity, have been made on one or a few kinds of animals at narrowly limited localities. The biogeographic significance of such work is evident, but as yet few studies have been made which seek to combine the facts of taxonomy, distribution, and ecology for a better interpretation of the relationships and distribution of a given group of animals. The study here reported on was conceived as such an attempt.

Early field experiences with the dusky-footed wood rat in California brought to my attention some of the attributes of wood rats which make these rodents especially well suited for biogeographic and evolutionary studies. Wood rats are sufficiently abundant, widespread, and diversified to indicate their success in adaptation to a wide variety of environmental conditions ranging from above the timber line on high mountains to true desert and from wet redwood forests to the High Plains. Morphologically, wood rats are plastic in external form, coloration, and osteological features. But in addition to these attributes, which are found also in a number of other groups of small mammals, wood rats are especially distinguished by their fondnesss for carrying home all sorts of objects picked up in their nightly forays. Such materials are used both as food and in the construction of conspicuous dens or houses for shelter and defense. These habits, which have earned for the animals the names pack rat and trade rat, are the bane of the camper and prospector who find their watches and silverware stolen, but the boon of the naturalist, who analyzes the contents of the house and middens, and is thus able to learn much about the shelter requirements and food habits of the occupant. Wood rats are among the few nocturnal animals which offer a convenient means of studying food and shelter relationships without the necessity of extended live-trapping and scat or stomach analyses at each locality.

The advantages of wood rats for ecological studies compare favorably with those of such diurnal animals as squirrels and rabbits that are more accessible to direct observation.

Of the nine species of wood rats (genus *Neotoma*) currently recognized north of Mexico, the ranges of six (*N. cinera, mexicana, albigula, micropus, floridana,* and *lepida*) extend into Colorado. This is a greater number than has been found in any other state. A seventh species (*N. stephensi*) has been taken within eight miles of the Colorado state line and may possibly occur at Four Corners, south of the San Juan River. An eighth species (*N. fuscipes*) lives only in the Pacific states, and the ninth (*N. magister*) lives only in the Appalachian region. The scope of the present problem has been limited to Colorado in order to allow study of the greatest variety of interspecific relationships within the modest limits of time and financial resources available. Colorado owes the great variety of its wood rats, as well as the variety of the rest of its fauna and flora, to the great diversity of physiographic and climatic conditions found within its borders. The wealth of environmental conditions offers ample opportunities for studying the distributional and ecological relationships of wood rats.

The study here reported on is concerned with the distribution of wood rats in Colorado: the local and geographic extent of their ranges, the factors limiting their spread, and the interspecific relationships permitting overlap of their ranges. It requires a sound taxonomic basis on which the ecological data may be organized and compared, and its conclusions help to make that basis more intelligible. Several years of nearly continuous study at any one locality would be desirable and necessary to obtain reasonably complete knowledge of the ecology of any one of the six species. But without some ecologic knowledge for all six species and for different parts of their ranges, an understanding of their distribution and relationships would not be obtained. It has been my aim to concentrate on the aspects of life history that I judge to be of greatest significance for the distribution of wood rats, namely local habitat, shelter, and food. Thanks to the collecting instincts of wood rats, such information can be readily obtained by analysis of their dens: their location, construction, and contents. Dens in many parts of Colorado and of all six species have been studied, with particular attention to localities at which the ranges of two or more species overlap.

Other aspects of life history such as behavior, reproduction, and growth of young received only occasional attention as opportunity permitted. Samples of ectoparasites were collected from each species and from various parts of the state, but the numbers obtained do not indicate the populations that were present on the wood rats.

ACKNOWLEDGMENTS

Without the assistance of many persons my study could not have been completed. I am indebted to the following persons for the loan of specimens in their care and for numerous other courtesies: Alfred M. Bailey and the late Albert C. Rogers, Denver Museum of Natural History; W. W. Postlethwaite, Colorado College Museum; David H. Johnson and Henry W. Setzer, U. S. National Museum; Stanley P. Young and Viola S. Schantz, U. S. Fish and Wildlife Service; H. E. Anthony, Hobart Van Deusen and the late G. H. H. Tate, American Museum of Natural History; William H. Burt and Emmet T. Hooper, Museum of Zoology, University of Michigan; Colin C. Sanborn, Chicago Natural History Museum; Hugo G. Rodeck, University of Colorado Museum; Seth B. Benson, Museum of Vertebrate Zoology, University of California; J. Kenneth Doutt, Carnegie Museum; B. P. Bole, Jr., Cleveland Museum of Natural History; William B. Davis, Agricultural and Mechanical College of Texas; and H. Radclyffe Roberts, Academy of Natural Sciences of Philadelphia.

I thank Mrs. Edward R. Warren for her kindness in making available to me the diaries and field notes of her late husband. Mr. Ansel F. Hall and Mr. Kenneth I. Ross extended to me the hospitality of the Explorers Camp headquarters in the La Plata Mountains and their field camp on Cahone Mesa. Numerous other citizens of Colorado, though they remain unnamed, are remembered for their friendly assistance that contributed to the success of the field work.

I am grateful to the following authorities for the identification of specimens of plants and invertebrates associated with wood rats:

Edward W. Baker	mites	Richard B. Loomis	chiggers
G. F. Ferris	lice	Curtis W. Sabrosky	warble flies
H. D. Harrington	plants	Ernest C. Smith	plants
William L. Jellison	fleas	R. W. Strandtmann	mites
Glen M. Kohls	ticks	Robert L. Usinger	cone-nosed bugs
Louis J. Lipovsky	chiggers	Marietta Voge	tapeworms

Figure 33 was drawn by Mr. Victor Hogg.

To Dr. Jean M. Linsdale and Mr. and Mrs. Russell P. Hastings I am indebted for the opportunity to seek an insight into the life of the dusky-footed wood rat on the Hastings Natural History Reservation. Without the inspiration and experience thus gained I would not have undertaken the present study. I acknowledge with gratitude the guidance and critical assistance of Prof. E. Raymond Hall throughout the course of the study and the preparation of the manuscript. I also extend thanks to Profs. Henry S. Fitch, A. Byron Leonard, Robert W. Wilson, and Raymond C. Moore for helpful suggestions and critical assistance.

To my wife, Eleanor, I am most grateful for encouragement and help with many routine but time-consuming tasks connected with the field work, museum study, and preparation of the manuscript.

MATERIALS AND METHODS

In the course of this study I examined 891 specimens of wood rats from Colorado representing 12 subspecies. In addition, many specimens from surrounding states were used for comparison. Specimens were examined from the collections named below and are listed under the accounts of subspecies by the following abbreviations:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BSC	Biological Surveys Collection, U. S. Fish and Wildlife Service
CM	Carnegie Museum
ClMNH	Cleveland Museum of Natural History
CNHM	Chicago Natural History Museum
DMNH	Denver Museum of Natural History
ERW	Edward R. Warren Collection, Colorado College
MVNP	Mesa Verde National Park
MVZ	Museum of Vertebrate Zoology, University of California
MZ	Museum of Zoology, University of Michigan
TCWC	Texas Cooperative Wildlife Collection, Agricultural and Mechanical College of Texas
UCM	University of Colorado Museum
USNM	U. S. National Museum

Specimens for which no collection is indicated are in the University of Kansas Museum of Natural History.

Reliable identification of the dens studied required capture of the resident wood rats and correct identification of each rat, whatever its age or condition of pelage, in order that significant observations on food, den construction, or other aspects of life history might not be attributed to the wrong kind of rat. Because a large proportion of the rats captured were not fully adult or not in fresh pelage, it was necessary to study the changes of pelage, skull, and dentition with growth and age, and to study the seasonal variation of pelage in adults.

In the section on variation, a discussion of general features applicable to all kinds of wood rats is presented under the following headings: secondary sexual, age and growth, seasonal variation, individual variation, and geographic variation. In the succeeding section, based on recognition of the different kinds of variation, I have discussed the characters having taxonomic significance under the following headings: size and external proportions, pelage, skull, and baculum.

The taxonomic section includes a brief treatment of each species of *Neotoma*, including synonymy, distribution, diagnosis, and comparisons.

The account of each subspecies begins with a synonymy, in which the first name combination is as given in the original description. The second name combination is that recognized herein. The following name combinations include in chronological order each separate combination that has been applied to wood rats from Colorado. Only the first reference and a few other more important references pertaining to wood rats of Colorado are cited under any name combination.

Following the synonymy, the type specimen and the type locality are designated. The range of the subspecies is defined, first in broad terms for its entire extent, then within Colorado. A diagnosis of the subspecies defines it briefly in terms of its most distinctive morphological characteristics.

I have described in some detail each subspecies known to occur in Colorado, hoping thus to facilitate the work of others who may have occasion to identify wood rats from Colorado or to study them in the field, and in order to present evidence for the taxonomic treatment used in the present work. The description of each subspecies is based as much as possible on the best series of adults in fresh pelage from the area in Colorado where the subspecies is most clearly differentiated. Specimens typical of various age groups and conditions of pelage differing from the basic descriptions are also described.

In the descriptions of pelage, capitalized color names and designators are those of Maerz and Paul, "A Dictionary of Color," 1930, unless otherwise indicated. Uncapitalized color terms are used without reference to any standard color guide, or sometimes to describe colors identified in Maerz and Paul only by number-letter-number designators of the plate, column, and row. Capitalized color names of Ridgway, 1912, are sometimes also given in parentheses and are invariably preceded by "R:". Where terms of Ridgway are used, they have been determined by direct comparison of the specimen with the color chip, not by comparison of the color chip with the plate of Maerz and Paul.

Tables of measurements for each subspecies are arranged together following the systematic accounts (see pp. 322-331). External measurements (total length, length of tail, length of hind foot, and length of ear) are those recorded by the field collectors. These measurements are given in millimeters, in a few instances having been converted from the collector's notation in inches and fractions or decimals thereof. Weights, when given, are those taken in the flesh by the collector and recorded in grams. Measurements of the skulls are in millimeters and tenths, as taken by the writer with dial calipers. The cranial measurements used in this study were taken in the same manner as described by Hooper (1938:216). In addition I have measured the diastema as follows: from the most anterior point on the alveolar border of the first upper molar to the most posterior point on the alveolar border of the upper incisor, wherever possible taken on the left side of the skull.

Under the heading "*Comparisons*" following the descriptions of each subspecies, the differences are pointed out by means of which the subspecies in question may be distinguished from others occupying adjacent ranges or that are of similar appearance.

The subsection entitled "*Remarks*" under each subspecies includes comments on particular localities, geographic variation, intergradation, individual variation, and abnormalities. Here are included any other details or observations related to the distribution, morphology, or taxonomy of the subspecies.

The probable geographic range of each subspecies is shown by a shaded area on one of the maps. Locality records of specimens examined by me are shown by means of solid circles. Additional records of occurrence (published records, specimens not seen by me, or dens that I consider definitely attributable to the species) are shown by means of hollow circles. All circles are numbered, in separate series for each subspecies; and each locality listed under "*Specimens examined*" or "*Additional records*" is preceded by an italicized numeral in parentheses indicating the appropriate circle on the map of that subspecies.

Localities only a short distance apart share the same circle and the same numeral.

In 1910 and 1911 knowledge of the wood rats of Colorado was notably advanced by the publication in quick succession of Goldman's "Revision of the Wood Rats of the Genus *Neotoma*" (1910), Warren's "The Mammals of Colorado" (1910), and Cary's "A Biological Survey of Colorado" (1911). More recently the second edition of Warren's book appeared (1942). These four works have been the references most helpful in my study, and the taxonomic treatment in each of the four publications is fully cited under the appropriate names recognized in the present work. Numerous other papers have been of value to me. Those cited in the text are listed at the end under *"Literature cited."*

The materials and methods employed for study of the ecology of the wood rats are described under the section entitled *"Ecology"* (see pp. 333-524).

PHYSIOGRAPHY, CLIMATE AND VEGETATION

Physiography.—Colorado is primarily a high-mountain state, including within its borders the greater part of the Southern Rocky Mountains. The elevation of the state ranges from 3350 feet at the lowest point, near Holly in the Arkansas Valley, to 14,431 feet at the summit of Mt. Elbert in Lake County. The average elevation of the state is 6800 feet (Gannett, 1906). There are 52 peaks in Colorado having an elevation of 14,000 feet or more; and there are 12,900 square miles (12.4 per cent of the total area of the state) above 10,000 feet, including more than a thousand peaks.

The eastern part (two-fifths) of the state extends out onto the Great Plains; and most of the western fringe, characterized by mesas, canyons, and valleys, is part of the Colorado Plateau Province. In contrast to the abrupt eastern limit of the Southern Rocky Mountains at the edge of the Great Plains, the western edge is ill-defined, merging irregularly with the Colorado Plateau Province south of the Yampa Plateau and with the Wyoming Basin Province in the northwestern corner of the state. (The names of physiographic provinces used herein are those of Fenneman, 1931.)

The Southern Rocky Mountains comprise a series of interconnected mountain ranges running mainly north and south, formed predominantly of crystalline rocks flanked by folded Paleozoic and Mesozoic sediments. Three principal east-west extensions of the Rockies project into western Colorado. These are the White River Plateau in northwestern Colorado, the Grand Mesa in the west-central part of the state, and the San Juan Mountains in the southwestern part. The Grand Mesa is a high (10,000 feet elevation) lava-capped mesa that is structurally a part of the Colorado Plateau but biotically a part of the Southern Rocky Mountains. Between some of the high mountain ranges are high, nearly level grassland basins or broad valleys. These are: North Park between the Park and Medicine Bow ranges, Middle Park between the Park and Front ranges, South Park between the Mosquito Range and Pikes Peak, San Luis Valley between the San Juan Mountains and the Sangre de Cristo Range, and Huerfano Park between the Sangre de Cristo Range and the Wet Mountains.

Colorado is traversed from north to south by the continental divide, and its mountains give rise to several major rivers of the western United States: the

North and South Platte, the Arkansas, and the Rio Grande draining into the Gulf of Mexico; and the San Juan and the Colorado draining into the Gulf of California.

The Colorado Plateau region of Colorado is characterized by predominantly horizontal Mesozoic and Cenozoic rocks bordered by escarpments and intersected by numerous deep, precipitous canyons. The rivers and principal tributaries from north to south are (1) the White River, (2) the Colorado and Gunnison rivers, (3) the Dolores and San Miguel rivers, and (4) the San Juan River tributaries. The Grand Valley of the Colorado River is the widest valley in western Colorado and is bounded on the north by the Book Cliffs and the Roan Plateau, a narrow western extension of the White River Plateau. The Grand Valley, continuous with the broad valley of the lower Gunnison River, is separated from the Dolores and San Miguel Canyons by the Uncompahgre Plateau, a broad nearly flat-topped uplift extending northwesterly from the San Juan Mountains.

The Wyoming Basin region of northwestern Colorado is largely open rolling sagebrush country with isolated mountains. It is drained by the Yampa River, which flows through spectacular gorges to its junction with the Green River near the western border of Colorado.

The Great Plains region of Colorado is an elevated plain rising from an average elevation of nearly 4000 feet along the eastern margin of the state to the base of the Rocky Mountain foothills between 6000 and 7000 feet in elevation. Two principal physiographic divisions are recognized, the High Plains on the eastern and northern border, and the Colorado Piedmont between the High Plains and the foothills. The High Plains section merges to the south with the Raton section of southern Colorado and northern New Mexico.

The High Plains is a smooth plain of low relief representing remnants of the formerly continuous, Tertiary and Quaternary alluvial mantle extending out from the Rocky Mountains. Its streams flow eastward following the original slope of the mantle. Its western limit is marked by the rim of a low erosional scarp which becomes, along the northern edge of the state, a line of precipitous bluffs and buttes. The Colorado Piedmont includes the drainage basins of the South Platte and Arkansas rivers and the interbasin divide. The Tertiary-Quaternary mantle has been almost entirely stripped off by the streams of the two drainage systems, leaving a maturely eroded rolling plain of low to moderate relief. The Arkansas-Platte Divide reaches a height of more than 7500 feet as a broad lobe extending eastward from the foothills and rimmed by steep bluffs and escarpments a few hundred feet high.

The part of the Great Plains south of the Arkansas Valley is essentially a high stripped plain continuous with the High Plains and rising westward to the mountains. The stripped plain is underlain by the resistant Dakota sandstone, most of the eastern part of which has been denuded, and through which the southern tributaries of the Arkansas River have carved rugged canyons. Closer to the mountains and the border of New Mexico, lava-capped mesas rise above the dissected plains.

Climate.—Colorado has a basically continental climate modified by the effects of high mountains. Characteristic features are low humidity, much sunshine, and wide extremes of diurnal and seasonal temperatures. These characteristics result from the prevailing westerly winds, the remoteness of Colorado from the Pacific Ocean, the reduced moisture content of Pacific air masses by the time they reach the state, and the failure of moist Tropical Gulf air masses to penetrate the state. Summer temperatures vary greatly with elevation, being generally high in the afternoon but cool at night. The maximum temperatures are closely related to elevation. Below 5000 feet, day temperatures frequently reach 100°F or higher in summer; but above 5000 feet, temperatures that high are rare. Winter temperatures are frequently low, with minimums occasionally less than –40°F in the mountain parks and Wyoming Basin. Night temperatures depend largely on the topography, air drainage frequently exerting a greater control than does the actual elevation.

The relative humidity is usually low at all seasons. Hence evaporation is rapid and soils are generally dry. Precipitation varies in different parts of the state, the lower elevations generally receiving much less than the high mountains. The precipitation occurs principally as snowfall in winter and thundershowers in summer. Some of the latter are of cloudburst proportions and result in local flash floods where slopes are steep and where rapid run-off is concentrated in shallow washes or narrow canyons. The amount of snow stored in the mountains is of great importance in replenishing ground-water supplies and maintaining the flow of streams. Because of the melting snow, most streams rising in the mountains are perennial. On the other hand, nearly all the smaller streams on the eastern plains that do not rise in the mountains flow only intermittently after heavy rains.

The climate of the high mountains cannot readily be briefly characterized because of the great differences in elevation and exposure to wind and sun within short distances. The summit of Pikes Peak has a mean temperature 35°F lower than that of Lamar, 10,500 feet lower in elevation. This difference in mean temperature equals that between Iceland and southern Florida. At elevations above 9000 feet frost may be expected in every month of the year. Although readings below zero in winter are commoner at high stations, the lowest temperatures in cold waves occur at the lower levels. The average precipitation on the higher parts of the San Juan Mountains and the Front Range exceeds 30 inches, compared with less than 10 inches in the Grand Valley and the San Luis Valley. The average annual snowfall at Cumbres, Conejos County, at 10,000 feet elevation, is 264 inches, whereas at Manassa, less than 30 miles northeast and at 7700 feet, the snowfall is only 18 inches.

Western Colorado, topographically diverse but of lower elevation than the high mountain masses, is distinguished climatically by the comparative uniformity of weather conditions from day to day. The high mountain masses that nearly surround western Colorado and eastern Utah deflect the paths of storms, with the result that those from the west usually cross the Continental Divide either north or south of Colorado where the divide is lower. In winter the severe cold waves that commonly sweep south over the Great Plains only infrequently cross the mountains into western Colorado. There is, rather, a tendency for a high pressure area to form and remain over western Colorado for days or weeks at a time. Under such conditions the skies are clear, the days mild, and the nights cold.

Although interior basins such as the mountain valleys retain cold air in winter and have temperature minimums as much as 40°F below zero, the lower valleys where drainage is good have much milder temperatures during cold spells. Near the mouths of large canyons where down-valley winds at night are strong, the night temperatures are mildest. The low valleys and canyons are also hottest and driest in summer. Precipitation occurs principally in winter and early spring, followed by a dry period in late spring and early summer. In late summer thunderstorms are common. Both snowfall and rainfall are greater at higher elevation and on slopes having a western exposure.

The climate of the Great Plains is characterized by low relative humidity; much sunshine; little rainfall, coming mainly in the warm season; wide extremes of temperature, and moderately high winds. The prevailing winds are northerly in winter and southerly in summer. Although the snowfall is light, it is usually swept in with a blizzard preceding a strong cold wave. The annual precipitation decreases from east to west, averaging near 18 inches at Wray and near 12 inches at Pueblo. The southern plains drained by the Arkansas River have a tendency toward drought in late spring and early summer. In unusually dry years the high winds common to that season sweep across plowed fields and blow away tons of fertile top soil, producing dust storms that obscure the sun.

The climate of the eastern foothills might be supposed to be intermediate between that of the mountains and the plains, but such is not quite the case. In winter the foothills are notably warmer than the mountains or the plains, and the wind movement is less. The mild winters are produced mainly by the prevalence of warm descending winds of the chinook type, and of mountain-and-valley type winds at the mouths of the main valleys. Below the mouth of the Royal Gorge the valley wind descending at night is sufficient to prevent the stratification of air in the Arkansas Valley and thus prevent the occurrence of severe cold over a considerable area.

Vegetation.—Colorado has a wide diversity of types of vegetation, which has been brought about by the diversity of topography and climate in different parts of the state. The most conspicuous and abrupt changes in vegetation are associated with changes in elevation. Other important factors affecting the distribution of plants are moisture, exposure to sun and wind, conditions of soil, grazing, and fire. The zonation of vegetation with elevation can be most clearly seen by ascending the Front Range from the edge of the plains to the summit above timber line. That this zonation is caused primarily by temperature is shown by the occurrence of the same belts or life-zones at lower elevations farther north and at higher elevations farther south. Life-zones are most easily identified by the presence of certain indicator species, usually trees or shrubs (Preston, 1940: xv-xx).

Five life-zones have been recognized with approximate limits in central Colorado as follows:

Arctic-Alpine	11,500-14,400 feet
Hudsonian	10,500-11,500 feet
Canadian	8,000-10,500 feet
Transition	6,000- 8,000 feet
Upper Sonoran	3,400- 6,000 feet

Although life-zones are best characterized by their floral assemblages, certain kinds of animals are also zonal in distribution. For instance, the white-throated wood rat (*N. albigula*) does not occur higher than the Upper Sonoran Life-zone in Colorado, whereas the Mexican wood rat (*N. mexicana*) occurs in the Upper Sonoran and Transition zones. The bushy-tailed wood rat (*N. cin-*

erea) occurs throughout all five zones but has one subspecies mainly occupying the upper four zones and two other subspecies confined to the Upper Sonoran Life-zone. Cary (1911) has described in detail the life-zones of Colorado and listed the zonal distribution of common plants and vertebrate animals.

The vegetation of Colorado may be usefully described also in terms of plant communities, which reflect the influence of all environmental factors, not just that of temperature. Each life-zone includes several major plant communities, some of which are very dissimilar in aspect, such as the spruce—fir forest and the mountain meadow, both in the Canadian Life-zone. A few communities have a wide zonal range, extending through two or more life-zones. The sagebrush community is widespread in the Upper Sonoran and Transition zones and in places reaches higher than 10,000 feet in the Canadian Life-zone. David Costello (in Harrington, 1954: iii-x) gives a good description of vegetation zones and plant communities in Colorado.

The highest zone, including the mountain tops above the upper limit of tree growth, bears a striking resemblance to the Arctic tundra and for this reason has received the name Arctic-Alpine Life-zone. Mosses, lichens, herbs and dwarf willows are abundant. Three communities are fairly distinct: the alpine summit community on exposed ridges and slopes with poor soil, the alpine meadow on more sheltered benches or gentle slopes with deeper soil, and the alpine willow community on low moist slopes near the lower border of the zone.

The narrow sub-alpine zone of dwarfed conifers at timber line and shortly below has been called the Hudsonian Life-zone. It is a transition belt between the treeless alpine communities above and the dense forests of Engelmann spruce and alpine fir below. In the sub-alpine zone stunted, deformed Engelmann spruce and alpine fir are the principal trees. Dwarfed limber pines and bristlecone pines occur more locally. The shrubs at timber line are taller and more luxuriant than those above.

The wide zone of montane coniferous forests and montane grassland is the Canadian Life-zone, including a considerable variety of plant communities requiring a cool climate with moderate rainfall or snowfall. The climax community is the spruce—fir forest dominated by the Engelmann spruce and alpine fir. Lodgepole pine forests form a more limited community in northern Colorado. Nearly pure stands of aspen are common on burned or cut-over areas. More open stands border grassland mountain parks. The sagebrush community, including rabbitbrush and antelope brush, is widespread on many drier slopes and over large areas of nearly level highland such as North Park, where it contacts the lower edge of the spruce—fir forest.

A belt of eastern foothills and western mountain slopes and mesas skirting all the high mountain masses is called the Transition Life-zone because it forms a transition from more humid boreal zones above to arid austral zones below. Much of the vegetation is a mixture of boreal and austral elements, but two species, the ponderosa pine and the scrub oak, have their greatest extent in the Transition Life-zone. The narrowleaf cottonwood is common along streams. The ponderosa pine—Douglas-fir association has two consociations, the ponderosa pine forest on drier south slopes and the Douglas-fir forest usually on north slopes. The former is usually more open and may be interspersed with aspen and grassland parks at higher elevations in the zone, or with grassland and scrub oak brushland at lower elevations. In western and southern Colorado the mountain shrub community forms detached thickets or narrow belts of brushland usually between one of the forest communities above and piñon—juniper or one of the semi-desert communities below. Dominants of the mountain shrub community are scrub oak, chokecherry, mountain-mahogany, serviceberry, antelope brush, snowberry, and skunkbush. In northwestern Colorado the ponderosa pine—Douglas-fir forest is replaced in the Transition Life-zone by mountain shrub on steep slopes and by sagebrush on the arid plains.

All of the lower valleys, canyons, and plains of western and eastern Colorado are part of the Upper Sonoran Life-zone. In northwestern Colorado the sagebrush community of higher zones extends down over the semi-desert plains of this zone on well-drained non-alkaline soils. In southwestern and southern Colorado the piñon—juniper woodland forms a distinct belt below the ponderosa pine—Douglas-fir forest and the scrub oak or mountain shrub communities. Piñons are absent and the stand of junipers is more open in the lower part of the belt. The piñon—juniper woodland covers much of Mesa Verde and the steep slopes of canyons in the San Juan and Dolores drainage systems, and it originally covered most of the upland divide between these two systems before the land was cleared for cultivation. In southeastern Colorado the piñon—juniper zone covers the flanks of the Sangre de Cristo Range and gives way to the short-grass plains below. In southwestern Colorado the piñon—juniper zone gives way to the semi-desert saltbush and greasewood communities that cover the poor alkaline soils of lower valleys and canyon bottoms. The greasewood occurs on the most alkaline, poorly drained sites whereas saltbush covers slightly higher drier soils.

Grassland communities of the Great Plains cover roughly the eastern two-fifths of Colorado. The natural climax vegetation was probably mixed prairie originally, but most of the area has been heavily grazed for so long that the short-grass disclimax dominated by blue grama and buffalograss is maintained. Taller grasses luxuriate only in low protected situations. The tree cactus is a conspicuous additional element of the short-grass plains over wide areas south of the Arkansas River and north as far as Fountain. A few shrubs, principally skunkbush, grow scattered on the banks of gulches and in shallow canyons. The sand sagebrush community covers large areas of loose sandy soil and dunes in many districts scattered over the plains. Groves of plains cottonwoods form an extensive community on the bottoms of the South Platte and Arkansas rivers, and scattered trees grow along smaller water courses.

GENERAL CHARACTERS OF *NEOTOMA*

Morphology.—Wood rats of the genus *Neotoma,* also called pack rats or trade rats, differ from the common brown rat (*Rattus norvegicus*) in appearance and especially in habits. The pelage of wood rats is soft and smooth and the under parts are usually white or buffy. The tail is shorter than the head and body. The tail is hairy or even bushy, and the annulations of small scales are scarcely visible without separating the hairs. The ears are large and scantily haired. The eyes are prominent. The vibrissae are long, frequently reaching the tips of the ears. The forefoot has four digits subequal in length; the pollex is rudimentary, without a claw.

The hind foot has five digits; four are subequal and the short hallux bears a claw. There are two pairs of inguinal mammae on the female.

Wood rats, like all cricetine rodents, have three molariform teeth in each jaw. The most distinctive character of the genus *Neotoma* is the structure of the cheek teeth. They are rooted and moderately high-crowned, thus occupying a position structurally intermediate between the low-crowned condition of *Peromyscus* and the high-crowned condition of *Microtus*. The enamel walls of the crowns of the teeth are folded inward on each side so as to divide the crown into a double series of enamel loops enclosing dentine and separated by enamel folds. On the flat occlusal surface of adult teeth the dentine is not completely divided into lakes by the enamel folds but remains in contact from one loop to the next. Tooth-wear in old age results in progressive obliteration of the folds.

The skull of *Neotoma* is moderately long and narrow. The rostrum is long, narrow, and parallel-sided. The maxillary root of the zygoma is notched above the antorbital foramen, but the lateral rim of the notch is not extended to form a spine on the upper margin of the zygomatic plate. The interorbital region is moderately constricted. The posterior half of the frontal suture is obliterated. The braincase is rounded and tapered anteriorly. The interparietal is wider than long. The incisive foramina are long, usually extending as far back as the anterior alveolar margins of the first molars. The interpterygoid fossa extends forward between the third molars. The bullae are oblique, tapering anteriorly. The coronoid process of the mandible is high.

Geographic distribution.—Most of the species and subspecies of *Neotoma* occur only in western North America. Two species, however, live in the eastern United States: *N. magister* in the Appalachian Region from western Connecticut to northern Alabama, and *N. floridana* through the southern states from the Atlantic coast of Florida to the plains of Texas and the Midwest. The bushy-tailed wood rat (*N. cinerea*) is distributed throughout the Rocky Mountain Region from southern Yukon to northern New Mexico. Several overlapping species range over all of the Pacific and southwestern states, northern Mexico, and the highlands from central Mexico to Nicaragua. The vertical range of the genus includes all life-zones from the Tropical coastal plain of Tamaulipas to the Arctic-Alpine of Colorado; but most kinds of wood rats occur in only two or three life-zones.

Ecologic status.—Three traits, present in greater or lesser degree in all kinds of wood rats, are primarily responsible for determining the ecologic niches of wood rats. These traits are climbing ability, the collecting of material for den construction or improvement, and a diet of predominantly leafy or succulent vegetation. Most wood rats are agile climbers, and two are especially so: *N. fuscipes* which is arboreal, and *N. cinerca* which is scansorial on high walls of cliffs and caves. *N. micropus,* at the other extreme, probably spends nearly all its time close to the ground level, although it does climb cactus, shrubs and low trees.

The instinct for collecting sticks, bones, cactus joints, scats and assorted man-made objects has given these animals a reputation for mischief wherever they find access to man-made articles in mountain cabins, camps, and ranch buildings. Although the gathering of such objects may seem aimless, the end result is usually an accumulation of a pile of debris having considerable protective value for the rat it shelters. The arboreal *N. fuscipes* has perhaps the best-developed collecting instinct and builds large stick houses three or four feet high. *N. cinerea,* being a cliff-dweller, has less need for a stick house because this rat finds good natural shelter in deep crevices and horizontal rock ledges. Most wood rats live either in rock crevices or in houses of sticks or cactus debris, according to the availability of rocks and suitable den materials. Other occasional types of shelter, such as hollow trees, burrows, or attics may be considered analogous to one or the other more usual types of dens. *N. mexicana,* which is most dependent on rock shelter for its dens, seems to have the weakest collecting instinct. According to popular belief, the "trade rat" brings sticks and other worthless objects to exchange for watches, silverware, or other articles in human habitations. Sometimes a person does find such a piece of trash in place of a lost article, but this usually happens when the rat, having picked up one object, chances upon another it likes better and cannot carry without dropping the first.

Wood rats eat a wide variety of plant food, depending on availability; but nearly always the foliage of trees, shrubs, and forbs is the dominant food through most of the year. The only major difference between species is the greater specialization of desert-dwelling species (*albigula* and *micropus*) for a diet of cactus pulp. Grasses seem to be of little importance except perhaps for short periods. Seeds, fruits, bark, and fungi are also eaten in season but are not the staple foods through most of the year. Wood rats forage mainly at night and store food in their dens for diurnal feeding and seasonal use. Adaptations for a diet of relatively coarse and unnutritious leafy vegetation are the high-crowned cheek teeth with increased enamel grinding surface and the much enlarged caecum for the breakdown of cellulose.

Economic status.—The economic status of wood rats cannot be unequivocally stated, because their activities seldom impinge directly on human welfare, and such activities have various effects, some beneficial, some harmful, and some neutral. Furthermore, the activities and their effects differ according to the kind of rat and a multiplicity of environmental conditions. A good discussion of the economic status of the white-throated wood rat in Arizona is given by Vorhies and Taylor (1940: 513-525). Much of their discussion would apply also to other kinds of wood rats.

Wood rats in Colorado are probably never an important economic factor. They eat a large proportion of the same plants browsed by deer and much less of the plants grazed by sheep and cattle. But the population of wood rats is seldom high enough to produce serious feeding pressure on the range. The damage and nuisance of wood rats about human habitations may at times be considerable. They are known also to be hosts of parasites capable of transmitting a few diseases, but such diseases are rarely, if ever, transmitted to man. On the other hand, wood rats are beneficial in promoting the fertility of the soil and may aid the extension of range of trees and shrubs by transporting cones, fruits and seeds. Mexicans and Indians of the Southwest have used wood rats abundantly as food and gather piñon nuts by raiding the storage caches of wood rats.

VARIATION

Secondary Sexual

Male and female adult wood rats of each species studied differ principally in size. Males average 5 to 10 per cent heavier than females. The length of head and body averages slightly greater in males. Lengths of tail, hind foot, and ear are usually about equal. Males and females do not differ in color when in comparable pelage. But the annual molt sometimes begins one to three months later in females than in males, probably because the onset of molt in some females is delayed until reproductive activity ends. The delayed molt in females often results in a conspicuous difference in the appearance of male and female rats taken in late summer. Males may be already in fresh new pelage with the annual molt nearly completed while females are still in old, thin and discolored summer pelage with the annual molt not yet begun or not sufficiently advanced to alter the rough appearance of the old coat.

The skulls of adult males are slightly larger than the skulls of adult females and frequently look to be more robust and angular. The males tend to have a larger rostrum, heavier zygomatic arches, more raised supraorbital ridges, and more prominent temporal ridges. These are, however, only average differences between the sexes. Almost any sizable series contains one or more females that surpass most, but not all, of the males.

Age and Growth

An understanding of morphological changes with growth and age is of great importance for comparing populations of closely related wood rats. Such changes present useful criteria by which individual rats may be arranged in order of relative age and divided into age classes for the convenience of description and comparison. Changes with age and growth, considered in relation to the seasons, also provide evidence for the recognition of the calendar age of individual rats, in terms of the year and approximate season of birth.

Specimens of young wood rats from Colorado are too few to permit a detailed study of age variation but are sufficient for the recognition of general trends, which are described briefly in the following paragraphs. A good account of cranial variation due to age, in *Neotoma micropus*, has been given by J. A. Allen (1894: 234) for specimens from Rockport, Texas. A detailed account of cranial variation due to age in *Citellus beecheyi* has been given by Hall (1926), who pointed out the general similarity of differential growth trends in *Citellus* and *Neotoma*. Growth and development of young wood rats of known age have been described for the following species: *fuscipes* by English (1923: 6), Linsdale and Tevis (1951: 393); *floridana* by Poole (1936: 25 and 1940: 265), Pearson (1952: 461), and Hamilton (1953: 182); and *albigula* by Richardson (1943: 130).

In the nestling wood rat the head and feet are large and the tail short, in comparison with the proportions of these parts in adults. The pinnae are at first folded over, closing the external auditory meatus, and the eyes are closed. The hairs of the juvenal pelage are short and still growing. Soon the pinnae become erect and the eyes open. With growth the tail becomes relatively longer until the adult size is reached. The length of the hind foot increases to nearly full size while the young rat is still in juvenal pelage and by the time it is one-third grown (by weight). The relative length of the hind foot, however, decreases because of the large size of the feet at birth. The ear grows rapidly, with increase in relative length as well as in absolute length, and reaches nearly full size at the same time as the hind foot.

PELAGES AND MOLTS.—Wood rats undergo at least two and frequently three molts in the first year and a single molt in each succeeding year of life. The names and succession of pelages and molts described below are: *Juvenal pelage, postjuvenal molt, subadult pelage, second molt, first autumn pelage, third molt, first winter pelage, annual molt.* More detailed descriptions and comparisons of the patterns and progress of molts are given under the ecological account of each species.

The hairs of the juvenal pelage are at first short, fine, and straight. They feel relatively stiff when separated by a needle. The ears are thickly haired both inside and outside. The pelage has a smooth, sleek appearance which it soon loses as the hairs grow longer. The back is generally some shade of gray or buff heavily overlaid with black, owing to the closely spaced black tips of the hairs. The sides are lighter, usually grayish washed with some shade of buff, according to the kind of wood rat. As the pelage increases in length the shafts of the hairs become wavy at the base, causing the pelage to become soft and fluffy by the time it is full length. With growth of the body, the hairs become more thinly spaced. The grayish basal coloration of the hairs shows through increasingly and the general coloration, therefore, becomes grayer and duller. Wear on the tips of the hairs may also contribute to the reduction of the black overlay and the decrease in richness of color on the sides.

The postjuvenal molt begins, usually, on the middle of the belly, or at separate centers on each flank close to the lateral line. From there it spreads as a wave over the body and reaches completion on the head. There is usually a molt line which is distinct under the covering juvenal pelage, if not on the surface. The progress of the molt differs somewhat in different kinds of wood rats, and even in individuals of the same subspecies. But in general the subadult pelage spreads rapidly over the belly and more slowly up the sides and hind legs until it meets first on the lower back. From there it spreads forward to the head. It seems doubtful that a complete change of hair occurs on the tail at the time of the postjuvenal molt.

The new subadult pelage differs markedly from the juvenal pelage in texture as well as color. The subadult hairs are straighter, and coarser than the juvenal hairs. They lie flat on the back, giving a smooth, over-all glossy appearance to the pelage, in contrast to the dull fuzzy appearance of the old juvenal pelage. The subadult pelage is usually buffier and less gray than the juvenal pelage but paler and less richly colored than the adult pelage.

A second molt takes place while the wood rat is reaching the adult condition (see p. 240). This molt begins in some species shortly before the completion of the postjuvenal molt, but in others sometime after completion of the postjuvenal molt. The second molt begins usually on the belly or near the lateral line and proceeds in the same general direction as does the postjuvenal molt. However, the progress of the second molt is more irregular, and it is more variable in different individuals and races.

The pelage acquired by the second molt may be called the *first autumn pelage,* since it ordinarily appears in the late summer or autumn of the first year. The first autumn pelage usually has the same texture as the subadult pelage but is richer in color. In *N. floridana* and *N. micropus* the subadult pelage is more fluffy, owing to the slightly wavy hairs, than the first autumn pelage, being intermediate in texture between the juvenal and first autumn pelages.

In most kinds of wood rats in Colorado, a third molt occurs in the fall or early winter of the first year. In the accounts that follow, the pelage acquired with the third molt in the first year will be referred to as the *first winter pelage.* Only in *Neotoma albigula* did I fail to find evidence of a third molt, but specimens taken in the fall are too few to establish whether a third molt occurs or not. The first winter pelage is usually like the first autumn pelage in color and texture but may grow longer and thicker in winter. Because the two pelages look so alike and the first autumn pelage is replaced before showing much wear, the third molt may be easily overlooked if the fur is not parted.

The acquisition of the first winter pelage may be considered the latest event in the sequence of changes with growth, and also the initial event in the seasonal cycle of the adult. The first winter pelage is retained through the first winter and is not replaced until the annual molt in the second summer or autumn.

Linsdale and Tevis (1951: 456) described the first autumn pelage of *Neotoma fuscipes luciana* in the following words: "The subadult [first autumn] pelage is darker dorsally than the adult and lacks the cinnamon color. Ventrally, the white of the subadult is more extensive than the white of the adult." Although for most kinds of wood rats in Colorado I did not distinguish any consistent difference between the first autumn pelage and later adult pelages, in some subspecies, such as *N. c. arizonae,* the first autumn pelage tends to be paler and less richly colored than subsequent pelages.

It may be noted here that the "immature pelage" and "subadult pelge" described by Linsdale and Tevis are the same as the "subadult pelage" and "first autumn pelage" respectively of the present report. Linsdale and Tevis did not recognize a third molt in the first year for the dusky-footed wood rat.

Old adults and seniles have the pinnae less haired than subadults and young adults, and usually have small tears or notches in the margins of the pinnae.

SKULL.—The skull of the nestling wood rat, in comparison with that of an adult, is relatively short, broad, and strongly arched in dorsal profile, with a relatively large smoothly rounded braincase. The sutures are widely open and some cranial elements (for example, the auditory bullae) are incompletely ossified. The rostrum and diastema are short, the zygomatic arches weak and deflected downward, and the basicranial elements are relatively small and crowded, in contrast to the expanded roofing elements of the braincase. The first two molars have erupted from the alveoli but have not reached full height. The palatal bridge is relatively well developed, in contrast to the basicranial region.

The median frontal suture begins to close shortly after birth and is obliterated for at least half its length by the time the molars show wear. The anterior end of the suture, for at least a quarter of its original length, remains visible throughout the life of the rat. Ossification of the bullae progresses rapidly to completion. The surface of the maxillary branch of the zygomatic arch does not become smoothly and fully ossified until the rat is almost fully adult. Sutures begin to close as the skull grows, but only the sutures in the occipital region become completely obliterated.

Growth of the skull is accompanied by changes in form and proportions. The greatest changes are associated with rapid elongation of the preorbital region and rapid growth of the basicranial elements, relative to the more slowly growing dorsal elements of the braincase. The dorsal profile becomes less arched, in adults of *N. cinerea* becoming almost straight. The diastema, length of nasals, and length of incisive foramen increase rapidly relative to the basilar length. The zygomatic breadth increases, at first rapidly as the zygomata move outward with growth. In later growth the zygomatic breadth increases more slowly but decreases relative to the basilar length. The breadth of rostrum increases absolutely but decreases relatively.

The least interorbital breadth changes but little in absolute measurements from birth to old age, but the relative interorbital breadth decreases greatly. The trends in actual measurements vary in different species. In *N. cinerea* the interorbital breadth remains constant or increases slightly in juveniles, immatures, and subadults, but decreases progressively in actual measurements in adults and seniles. In *N. mexicana* and *N. albigula* the interorbital breadth increases slightly in juveniles, immatures, and subadults; it remains nearly constant or may decrease slightly in adults and seniles. The palatal bridge also changes little with age but decreases in relative length until the skull is full grown.

Changes in form and proportions of the skull as a whole are, of course, accompanied by many changes in the component elements of the skull. The interparietal is particularly variable with growth, as has been well shown by J. A. Allen (1894: 236) for *N. micropus micropus*. In general, for all species of *Neotoma* in Colorado, the interparietal in young rats is more transversely elliptical or rectangular than in adults, in which the shape varies but is less expanded transversely relative to the length in the longitudinal axis. In spite of great individual and age variation of the interparietal, this element furnishes some useful differences between certain species and subspecies.

After the rat has reached full adult size a few gradual cranial changes continue. The supraorbital ridges become sharper laterally, especially in *N. micropus* and *N. floridana*. The temporal ridges and other places of muscle attachment become more prominent. In *N. cinerea, N. micropus, N. floridana* and *N. lepida* the frontals become more channeled in the interorbital region.

DENTITION.—The dentition provides the most reliable criterion for the recognition of age in wood rats, because the molars are moderately high-crowned and subject to a measurable rate of wear, terminating with destruction of the crowns and exposure of the roots. The molars erupt in sequence from front to back, the first and second molars emerging from the alveoli nearly at the same time in the nestling rat. When the crowns of the first and second molars have reached nearly full and equal height, the third molars erupt from their alveoli. As the third molars grow, the first signs of wear appear on the first and second molars. The third molars show no wear until they have reached the same height as the other teeth in the row. The lower third molars seem generally to reach occlusal height a little later than the upper third molars, and after these already show some wear. The initial wear on the M3s must be produced by abrasion against the m2s in longitudinal chewing movements of the mandible.

In this connection it may be mentioned that the rate of wear on the upper and lower molars is completely independent of the wear on the incisors. A. B. Howell (1924: 1011) expressed a different view concerning tooth wear in *Microtus montanus yosemite:* "The length of the anterior molars in relation to the posterior ones, in both upper and lower series, is, of course, interdependent upon the length of the incisors and the configuration of both the upper and lower diastemata. . . . Longer incisors . . . would . . . effect longer anterior cheek teeth, for these latter cannot wear down more rapidly than the wear of the incisors permits." Examination of the occlusal relationships of upper and lower molars and incisors, and the nature of the mandibular articulation with the squamosal, show that such is not the case in wood rats. When the molars are in normal occlusion, the tips of the lower incisors overlap the upper incisors posteriorly without touching them. For the lower incisors to occlude with the pits on the upper incisors, in the normal position for gnawing, the lower molars must be separated from the uppers and moved forward. A cursory inspection of skulls of *Microtus montanus* shows that the same relationship holds.

The crowns of the molars are widest at the base and taper slightly toward the tips. Also, the thickness of individual lophs is greatest at the base and becomes less toward the tips. Consequently the spaces in enamel folds (between lophs) are greatest near the tips and become nearly closed at the bases of the crowns. These proportions result in an increase in the area of surface for grinding food as the rat grows older, and an increase in the width of dentine exposed at the occlusal surface of each loph. After the crown is worn down to its base, this trend is reversed as wear progresses into the neck joining the crown with the roots. The progressive emergence of the molars and the attrition of their crowns with age can be seen in lateral view as a change in angle of slope of the posterior face of M3. In the subadult rat the posterior face slopes forward from the alveolus; in the early adult the posterior face is nearly vertical; and in the late adult the posterior face of M3 slopes backward and parallel to the anterior face of M1.

Wear on the crowns of the molars appears first as small polished surfaces on the most projecting parts of the enamel wall. As the polished areas increase in area they soon cut through the enamel into the dentine, and the polished enamel spreads as a line outlining the occlusal surface of the loph or the entire tooth. At first there are pits extending down into the dentine within each loph or enamel loop, and the dentine of adjacent lophs is interrupted. As wear progresses, the pits become smaller and the dentine joins continuously over the occlusal surface of the entire molar. In the mature condition of dental wear the polished enamel forms a single closed and folded line around the entire tooth, and the polished dentine continuously fills the area within the enamel line, all pits having been obliterated. When wear is still at an early stage on M3, it is usually nearly mature on M1 and M2, but with persisting small pits in some lophs. As wear approaches the mature pattern on M3, the pits in the dentine of the posterior lobe may be the last sign of immaturity to disappear, or in other specimens the enamel walls of adjacent lobes may remain separate and may not close to form one outline until after obliteration of the last pit. In most specimens m3 does not reach the mature condition of wear until after all upper molars are mature.

The enamel folds on the molar crowns extend down the sides of the teeth for the full lengths of the crowns. In most species the bases of the enamel folds do not emerge from the alveoli until after the occlusal patterns have reached full maturity. But in some individuals of *N. micropus canescens*, *N. albigula warreni*, and *N. cinerea rupicola* the bases of the enamel folds emerge from the alveoli shortly before the M3 patterns attain complete maturity. Full emergence of the molar crown is followed by emergence of the narrow neck of the tooth, then increasing exposure of the roots.

In late maturity the inner angles of some enamel folds become cut off on the occlusal surface by contact of the opposing enamel walls to form hollow enamel lakes. In some subspecies a lake is formed by the posteroexternal fold of M3 much earlier than by any other fold, even in the early adult. In old rats, after almost the entire crown has been worn away, all folds are reduced to lakes and these are finally worn away. The enamel wall of the molar extends down the sides of the tooth only approximately to the base of the enamel folds, or even less on the outer sides of the lophs. In the lakes the enamel usually extends a little lower into the tooth than on the sides. When the tooth is worn down to such a level that there is a break in the continuity of the enamel outline, abrasion cuts into the dentine and progresses more rapidly at that spot. The occlusal surface becomes rounded at the side in contrast to the sharply elevated rim formed by enamel. The uneven, irregular grinding surface of senile rats is due to the uneven lower limit of enamel and the differential rates of wear of enamel and dentine.

In most old rats the enamel disappears on the anterior face of M1 sooner than on the anterior face of m1. As soon as this happens, almost all subsequent abrasion occurs on the anterior dentine of M1 while the opposing enamel of m1 remains almost without further wear. Only the anterior enamel lakes of M1 stand up like dikes resisting the wear of the nearly intact enamel outline of m1. With final disappearance of the enamel lakes, disintegration of the tooth proceeds rapidly until in extreme senility even the roots of the tooth may break apart. The more rapid attrition of the anterior end of M1 results in a curved plane of occlusion with the anterior end bending dorsally. In instances of extreme wear M1s have the enamel pattern half gone while M3s still have normal mature patterns with low crowns and m1s have medium crowns curving upward anteriorly to high sharp points.

In young wood rats the alveolar length of the maxillary tooth-row (the length of the alveoli, not the molar crowns) remains nearly constant after the eruption of M3 until the animal is adult. At first the teeth fit loosely in their sockets. As the largest parts of the crowns emerge, the space between the teeth and the alveolar rims of the maxillary is closed. With increasing age of the adult, the length of the teeth at the alveoli decreases as the narrower necks of the molars emerge until the roots become exposed. The alveoli close in around the teeth and anchor them solidly in their sockets, resulting in a gradual decrease in the actual measurement of the alveolar length during adult life. The alveolar margins are thin and sharp in young rats but become progressively more rounded and blunt with erosion or dissolution of the bone at the line of contact with the teeth. In old age this trend, together with greater exposure of the diverging molar roots, results in a slight increase in alveolar length of the maxillary tooth-row. The relative alveolar length of the tooth-row is large in young wood rats and decreases rapidly until the animal is grown. After that it decreases at a slower rate until old age, when the trend may be reversed by a slight increase in the relative alveolar length.

Because it changes so little during the life of the individual rat, the alveolar length of the maxillary tooth-row is especially useful as a taxonomic character for the identification of young specimens.

Nestlings of *Neotoma fuscipes* in California have the tips of the incisors sharply recurved and diverging to form opposing V's (Vestal, 1938: 23). The condition is illustrated by Lawrence (1941: 315) and by Linsdale and Tevis (1951: 396). The same condition is described for *N. floridana* by the Svihlas (1933: 75) and for *N. albigula* by Vorhies and Taylor (1940: 477). Such modified incisors have been interpreted as adaptations enabling the young to cling more tenaciously to the mother's nipples. I have seen juvenal skulls, with no tooth wear, of *N. cinerea rupicola, N. mexicana inopinata,* and *N. floridana campestris.* The first two subspecies showed no modification of the upper or lower incisors except a slight shallow groove on the anterior tip of each upper incisor. *N. f. campestris* has slightly modified incisors. The uppers are each grooved on the anterior face and tip, but do not diverge distally; the lowers are slightly recurved but do not diverge.

In studying museum skins and skulls of wood rats I have found it convenient, for description and comparison, to recognize the age classes briefly described in the following paragraphs. The general scope of each class is thought to represent a fairly natural biological segment of the life span, but the limits of the classes are artificial and were set where conveniently sharp structural changes can be recognized. The classes are defined primarily on dentition because it provides good recognizable age differences throughout the life span of the individual. Other useful criteria are provided by cranial sutures. The evidence from the sutures, in some specimens of marginal age, however, does not always agree with that from the dentition. The statements in the following paragraphs concerning actual age, length, weight, and pelage are given as general descriptions of the respective classes but are subject to wide variation.

Juvenile.—Nestling or suckling stage. From 0 to 3 weeks of age; length of head and body up to 110 ± mm and weight up to 50 ± grams in *N. cinerea.*

Skull: First and second molars erupting from the alveoli but showing not more than a trace of wear, not sufficient to form a closed loop of polished enamel on any molar; median frontal suture complete.

Pelage: Juvenal pelage growing, but not yet full length; hairs short, fine, and straight, giving a smooth, sleek appearance to the pelage.

Immature.—Playing and weaning stage. From 3 to 8 weeks of age; length of head and body 110 ± to 180 ± mm and weight 50 ± to 150 ± grams in *N. cinerea.*

Skull: First and second molars fully erupted and sufficiently worn to form a loop of polished enamel on at least one upper molar; third molars erupting but showing no wear; median frontal suture fused for part of its length.

Pelage: Juvenal pelage fully grown; hairs long, fine, soft, and wavy toward the base, giving a soft, fluffy appearance to the pelage; postjuvenal molt under way late in the period, with subadult pelage visible low on the sides but covered by juvenal pelage on the back and rump.

Subadult.—Stage of establishment of own den and attainment of sexual maturity. From 2 to 4 months of age; length of head and body 170 ± to 230 ± mm and weight 150 ± to 300 ± grams in *N. cinerea.*

Skull: All upper molars fully erupted; third molars showing at least a trace of wear, but occlusal pattern of wear not fully mature; exoccipital sutures not obliterated.

Pelage: Postjuvenal molt in full progress or virtually completed, but end of tail in *N. cinerea* still whitish and tufted, not bushy; juvenal pelage usually unreplaced on nape or crown until the close of the period; subadult pelage externally visible at least on sides and hips, then covering the entire body; second molt usually beginning low on the sides late in the period.

Adult.—Stage of cyclic reproductive activities, attainment of full size and full vigor. From 4 months to 2½ years of age; length of head and body 180 ± to 250 ± mm and weight 175 ± to 440 ± grams in *N. cinerea.*

Skull: Each upper molar with continuous outline of polished enamel; dentine interconnected between lobes and containing no pits in the surface; enamel folds of molar crowns all present, not eliminated by wear; exoccipital sutures fused and obliterated.

Pelage: Subadult pelage covering most of body at the start of the period; second molt taking place in first autumn, followed usually by third molt; first winter pelage retained until annual molt in second summer; a single annual molt each succeeding year.

Senile.—Stage of old age and declining physical condition. More than 2½ years of age; length of head and body 215 ± to 250 ± mm and weight 225 ± to 400 ± grams in *N. cinerea.*

Skull: Roots of molars well exposed; enamel folds barely visible on sides of molars; mature occlusal patterns of upper molars modified by wear with the loss of at least one enamel fold and the progressive reduction of others. Modification of the patterns proceeds, first, by isolation of the enamel folds as lakes on the occlusal surface, then by complete elimination of the lakes.

Pelage: Not distinguishable from pelage of adults; the face usually more scarred and thinly haired, the pinnae almost naked.

Seasonal Variation

The cycle of changing seasons affects wood rats in many ways, perhaps the most important of which concerns the reproductive cycle. Seasonal changes in feeding habits, daily activity, and body weight are also of undoubted importance in the life of the wood rat.

But for the identification and comparison of specimens we are concerned here primarily with the seasonal variation in appearance and condition of the pelage.

Insofar as different species have been studied, there is evidence of only one annual molt in adult wood rats. The annual molt generally occurs in the late summer or autumn and requires several weeks to progress to completion. The differences between "winter pelage" and "summer pelage" are the result of a thinning of the fur by partial shedding, shortening of the hairs by wear on the tips, and alteration of the hair pigments (perhaps oxidation and fading) by exposure to light and other environmental factors. The fresh new pelage in early winter is long and dense. Its texture is smooth and soft, and its coloration is usually rich and fresh. When the fur is ruffled the skin is barely visible between the hairs. The black tips of the hairs on the upper parts are ordinarily longer than in summer, giving the appearance of a heavier overlay of black on the back. The white tips of the hairs on the under parts are longer, giving the appearance of more solid white covering the gray basal color of the hairs.

The condition of the pelage shows little change on specimens taken on various dates through the winter and early spring. In late spring and early summer the condition and appearance of the pelage changes markedly, seemingly within a period of only a few weeks. The fur thins out, wears shorter, and changes color, usually becoming more brownish or reddish and less heavily overlaid with black on the back. By midsummer the pelage is noticeably thin, so that when it is ruffled, much skin is exposed between the hairs. The fur appears rough because of the unevenness of shedding, where little patches of hairs have pulled out. The roughness is especially noticeable on the lower back, rump, and hips. The fur on the back feels shorter and stiffer than fresh new pelage. The stiffness is partly, at least, a consequence of the shortness of the hairs, but may also indicate a dryness and brittleness which could account for the increased wear on the tips of the hairs. The heavily worn pelage in midsummer is duller, less richly colored on the sides, and less black on the back than fresh "winter pelage." Heavily worn pelage is usually more brownish, with sometimes a more rusty or reddish tone. The white on the belly is thinner, exposing more gray basal coloration.

The annual molt usually begins in patches and spreads irregularly over the body. Often the fur seems to come in first in those patches where the old fur is thinnest or has completely dropped out. Excessive wear of the old pelage, particularly in males, may stimulate the early and irregular onset of the annual molt, perhaps in the same manner as the accidental loss of the tail feathers of a bird stimulates their rapid replacement.

The picture of seasonal variation in pelage presented above was seen most clearly in *Neotoma cinerea orolestes,* of which race I have the greatest number of specimens from all seasons of the year. Evidence from other species is less complete, or even scanty; but the general pattern seems to be the same, although the seasonal differences in some subspecies are less extreme.

The importance of recognizing seasonal differences in pelage, when comparing related geographic races, seems too obvious to require emphasis. Whenever possible it is desirable to describe and compare kinds of mammals on the basis of adult specimens in fresh unworn pelage. Only thus can the effects of exposure to varying climates and other conditions be eliminated. Unfortunately, in wood rats, as in most other kinds of mammals, the season most favorable for obtaining animals in fresh pelage comes in late fall and winter when few collectors are in the field. In the absence of specimens in prime "winter pelage," one can only compare the best or most similar skins at hand and make allowances for the probable effects of seasonal variation.

Individual Variation

Among specimens of a single species from any limited area, grouped according to sex, age, and season, a considerable degree of variation can be seen which may be conveniently referred to as individual variation. Under this term is included that residue of variation remaining in a species after elimination of variations due to sex, age, season, and geographic origin. The differences here referred to may be inherited or may be the result of environmental influences affecting the life of the individual rat. Some characteristics are subject to all five kinds of variation. Thus size (as indicated by length of head and body, weight, and basilar length of the skull) increases with age of young, differs between adults of opposite sex, fluctuates with season under the influence of the reproductive cycle (Linsdale and Tevis, 1951: 346), differs between individuals of the same sex and age taken at the same place on the same day, and may show average differences between adults of the same sex, age, and season collected at widely separated localities.

Some characteristics of wood rats are subject to only one or two kinds of variation. For instance, the presence of an anteroexternal enamel fold on the m3 was mentioned by Merriam (1894: 124) as one of the characters on which he based his description of *Neotoma fallax* as a distinct species. Later Goldman (1910: 57) pointed out that the anteroexternal fold of the m3 "occurs irregularly in nearly all of the members of the *mexicana* group." He reduced *fallax* to a subspecies of *N. mexicana*. The extra fold thus has no specific or geographic significance. Counts of the frequency of its occurrence in the three subspecies of *N. mexicana* in Colorado (see under "*Remarks*" in the respective accounts of subspecies) show that it occurs in roughly one third to one half of the specimens from any part of the state, irrespective of age, sex, or season. The depth, as well as the presence, of the anteroexternal fold of the m3 varies from individual to individual, although the exposure of the fold at the occlusal surface of the molar changes with age and wear. Since the enamel pattern of the molars is laid down in the embryonic stage, the presence or absence of the extra fold is almost certainly hereditary.

Some of the features subject to great individual variation are: length of head and body, length of tail, weight, general coloration, extent of gray basal color on fur of under parts, size of skull, length and shape of nasals, length of dorsal extensions of premaxillaries, shape of parietals, size and shape of interparietal, length of incisive foramina, length of palatal bridge, shape of interpterygoid fossa, length and breadth of sphenopalatine vacuities, size and shape of auditory bullae, and size of teeth. By no means all of the above features show wide individual variation in every population of wood rats. Some features are more variable in one species, and other features are more variable in other species or local populations.

Features which vary individually, such as size, color, and shape of interpterygoid fossa, may also furnish useful differences for distinguishing subspecies or species, provided the geographic or interspecific differences exceed the individual difference. But the variations of such features due to sex, age, season, and individuality must be distinguished before the geographic or interspecific variation of these features can be recognized and used to identify wood rats.

Geographic Variation

Each of three species of wood rats has an extensive distribution in Colorado and shows geographic variation sufficient to warrant the recognition of more than one subspecies. Three other species show no geographic variation in Colorado, but do vary much outside the state. Two of these (*N. lepida* and *micropus*) have only limited ranges in Colorado. The third (*N. floridana*) has a rather wide range over the Great Plains where conditions are fairly uniform and uninterrupted by barriers.

Some of the features more variable geographically are size of body, color of pelage, size and shape of skull, length of rostrum, shape of frontals, configuration of temporal ridges, shape of interparietal, shape of bullae, size of incisors, and length of maxillary tooth-row. Many of these features are also notably variable with age, especially size, color of pelage, shape of skull, length of rostrum, and shape of interparietal. In many cranial characters, second year adults of *N. cinerea arizonae* from southwestern Colorado resemble subadults or first year adults of *N. orolestes* from central Colorado but are clearly different from second year adults of *orolestes.*

Geographic variation of color is greatest in *N. cinerea. N. c. orolestes* is darker than the other two subspecies in Colorado and inhabits the higher montane habitats in the central part of the state. The darker color of *orolestes* is correlated with cooler, more humid climate. *N. c. arizonae* and *rupicola* both are much paler than *orolestes* and live in low semiarid habitats in the western and northeastern parts of the state, respectively.

In *N. albigula* there is marked difference in color between specimens from southwestern Colorado and specimens from southeastern Colorado. Those from the southeast are more gray, resembling *N. micropus* in the same area. There seems to be no correlation of coat color with any environmental factor. In *N. mexicana* there is only slight geographic variation in color within Colorado. Specimens from the eastern foothills north of the Arkansas River tend to be darker, and less richly colored on the sides, than specimens from southeastern and southwestern Colorado. In the San Luis Hills an unusual pattern of dichromatism occurs in *N. mexicana* (see p. 282). About half the specimens from three miles west of San Acacio have darkly pigmented feet, tail and venter. Normally-colored specimens from the same area are little, if any, darker than specimens from the southeastern foothills.

Coloration of wood rats of Colorado seems to have little relation to color of the substrate. The colors of rock formations and soil types are much more varied than the colors of wood rats, and rocks of contrasting colors frequently occur together in the same canyon or on the same mountain mass. In southeastern Colorado *N. micropus canescens, N. albigula warreni,* and *N. mexicana scopulorum* occur at the same localities. The first two subspecies are similar in color and much grayer than *scopulorum,* and grayer than the Dakota sandstone, which provides much of the favorable wood rat habitat in the region. Furthermore, the only habitat separation sometimes occurring is between the two gray subspecies, *canescens* and *warreni. N. m. canescens* is more often found in cactus houses on open valley floors, and *warreni* more often in rock outcrops where the more brownish *scopulorum* also occurs. In southwestern Colorado three other subspecies occur together at many of the same localities. *N. albigula laplataensis* and *N. mexicana inopinata* are practically identical in color and nearly the same as *scopulorum* in southeastern Colorado. *N. cinerea arizonae* is brighter orange buff and lives in many of the same rock outcrops as *laplataensis* and *inopinata.* The upper sandstone member of the Dakota formation, which is widespread and uniform in color in both western and eastern Colorado, provides shelter for wood rats of nine different kinds (*N. c. orolestes, N. c. arizonae, N. m. fallax, N. m. scopulorum, N. m. inopinata, N. a. laplataensis, N. a. warreni, N. m. canescens,* and *N. l. sanrafaeli*) having at least five recognizably different colorations.

Geographic variation of cranial features in *Neotoma cinerea* has principally a northeast-southwest trend, with secondarily a north-south trend in the western part of Colorado. *N. c. rupicola* in northeastern Colorado has a large, robust, and angular skull with large rostrum, large upper incisors, wide interpterygoid fossa, and large inflated bullae. *N. c. orolestes* in central Colorado has a somewhat less angular skull with narrower rostrum, narrower upper incisors, narrower interpterygoid fossa, and narrower, less inflated bullae. *N. c. arizonae* in southwestern Colorado has a smaller smoother skull with a shorter and narrower rostrum, narrower incisors, wider temporal ridges, and wider interparietal. But the trends of the interpterygoid fossa and bullae are reversed, being wider and more inflated, respectively in the southwest, as in the northeast, when compared with the central *orolestes.* These changes are rather abrupt between the ranges of the subspecies and do not form clines. There seems to be no general north-south trend of variation in *orolestes.* But in *arizonae* there is a slight clinal trend from south to north. The size of the rostrum and upper incisors increases toward the north, and the length of the dorsal branches of the premaxillaries averages greater in the north.

Neotoma mexicana shows separate local trends in size of skull in different parts of its range. In general the skulls tend to be smaller toward the north, both in eastern and in western Colorado. In eastern Colorado they also tend to be smaller toward higher elevations (west) and larger toward lower elevations (east), with a correlated trend in size of rostrum and upper incisors, which are smaller toward the north and higher elevation. The trend of the upper incisors is more extensive geographically, ranging from large and pale in the southeastern corner of the state to intermediate in the eastern foothills of the Rockies and smallest and most orange along the western border of the state. The posterior width of the temporal is greatest in the eastern foothills north of the Arkansas River and becomes more variable in the southern parts of the state. In western Colorado the temporal is generally narrower but also rather variable. *N. m. scopulorum* in the southeastern corner of Colorado seems to be a terminal population having a few characters more strongly developed than in any other part of the state. Thus, the skull is more arched at the base of the rostrum, the interorbital constriction is more posterior, and the interparietal is shorter and more rectangular. Mexican wood rats with the most nearly round and most inflated bullae are from the San Luis Hills and the margins of the San Juan Mountains in southern Colorado. Along the southwestern border of the state the bullae are round but not so large. In the eastern foothills and the southeast the bullae are generally small and narrow. Nasals reaching farthest posteriorly are found in skulls from the San Luis Hills, where they frequently extend beyond the dorsal branches of the premaxillaries. This extreme was almost never seen in skulls from west of the Rio Grande, and only occasionally in skulls from southeastern Colorado.

Specimens of *N. mexicana* from the San Luis Hills do not fit, as I had expected them to do, into a geographic trend as intermediates between specimens of the southwest and those of the eastern foothills. Instead they are more like specimens from the southeastern corner of the state. However, they show a few trends different from those in either the southwestern or southeastern parts of Colorado, such as dichromatism (see p. 282), shorter tail, more posterior extension of nasals, and larger maxillovomerine notch.

The only cranial characters of *N. albigula* that show a seemingly general trend involving all three subspecies in Colorado are the size of the upper incisors and the width of the rostrum. These are greatest in *brevicauda* in western Colorado and least in *warreni* in southeastern Colorado. This trend is the reverse of the one present in *N. mexicana* over the same area. More limited geographic variations in cranial characters seem to have resulted from the partial isolation of *brevicauda* and *warreni* and their marginal positions in relation to the main range of the species.

TAXONOMIC CHARACTERS

Size and external proportions

Wood rats differ greatly in size, that is to say, length and weight of the animal, but such differences are due to many causes which reduce the taxonomic usefulness of size. Marked differences were found between individuals of the same sex and age from the same locality. Linsdale and Tevis (1951: 337) have shown that such differences in the dusky-footed wood rat can be correlated with favorable and adverse conditions in the life histories of individual rats, such as the residence or disappearance of a dominant competing male at an adjacent den. In general, in a limited region such as Colorado, size has greater taxonomic value for distinguishing species than for distinguishing subspecies. This is so because the magnitude of difference in size between species more clearly exceeds differences due to other factors.

Of the external measurements, the length of the hind foot is most useful taxonomically, because the full length of the foot is attained at a relatively early age and seems not to be greatly affected by differences in body size. The length of the ear also is a useful measurement showing significant taxonomic differences. Unfortunately, this measurement was not taken by early collectors, and measurements taken from the dry skin are too variable to be reliable. Length of the tail is markedly variable in wood rats and of little taxonomic value. It is especially subject to accidental shortening, as well as to high individual variation.

Pelage

Between some species there is noticeable variation in length and texture of pelage when specimens of similar age, sex, and season are compared, but between subspecies of the same species there is scarcely any difference. Color is useful in distinguishing some species and subspecies of wood rats but must be used with caution. The general color effect is produced by a pigmented terminal or subterminal color band on the overhairs, a generally grayish basal coloration of the overhairs, and the long dark-tipped guard hairs which overlie the overhairs in varying length and density. (No underfur is present.) Differences in general color appearance result from differences in the lengths and proportions of these components as well as from differences in the actual pigments present. Color is highly variable in most populations and can be used taxonomically only by comparing specimens closely similar in age and condition of pelage. The differences between some subspecies are greater than those between some species. Such differences as can be recognized by the eye are usually subtle and can be expressed only crudely by word description. Reference to published color standards gives a better notion of the difference but is far from satisfactory. Color pattern is more useful than general coloration, especially for distinguishing species. A dark line or band around the mouth is almost invariably present in *N. mexicana* and absent in other species. A dark eye ring is usually also present but less distinct in *mexicana*. The presence and size of an area or patch of pure white hairs on the breast has taxonomic significance. But the presence and intensity of a buff pectoral band is subject to much individual variation, and in rats from Colorado is not sufficiently constant for taxonomic use.

Skull

The skulls of wood rats present numerous variable features, many of which have taxonomic value. Some of the more useful features are: size of skull, general form, degree of arching in lateral aspect, length and breadth of rostrum, shape and breadth of zygomatic arches, shape of interorbital region, prominence and pattern of temporal ridges, length and shape of incisive foramina, condition of nasal septum, shape of anterior palatal spine, shape of posterior margin of bony palate, width and form of interpterygoid fossa, presence and size of sphenopalatine vacuities, size and shape of auditory bullae, width of upper incisors, size and proportions of molars, length of maxillary tooth-row, and depth of anterointernal enamel fold of M1. A few features which have not been described previously are sufficiently useful to merit some explanation.

By "condition of nasal septum" is meant whether the bony septum is intact or separated from the anterior palatal spine by a deep notch. When intact, the septum is visible through the incisive foramina as a thin but solid partition of bone (the vomer) in the median plane and separating the right and left nasal cavities. The vomer is in continuous contact ventrally with the anterior palatal spine (formed by the maxillaries) and the corresponding processes of the premaxillaries. The posterior edge of the vomer, when intact, lies dorsal to the palatal bridge and can sometimes be seen by looking at an angle posteriorly through the incisive foramina. When the nasal septum is notched, the vomer is separated posteriorly from the maxillaries but is still in contact anteriorly with the premaxillaries.

The notch (hereafter referred to as the *maxillovomerine notch*) is clearly visible through the incisive foramina and looks like a fenestra in the septum, except that the posterior end, dorsal to the palatal bridge, remains open. The maxillovomerine notch is, thus, merely an anterior extension of the posterior margin of the vomer. The presence or absence of a maxillovomerine notch is a highly reliable specific character, at least in Colorado. The length, width (depth dorsoventrally), and shape of the maxillovomerine notch are useful subspecific characters in at least one species, *N. albigula.*

Specimens of all species of wood rats north of Mexico have been examined to ascertain the conditions of the nasal septa. *N. floridana* and *N. micropus* have the septum intact (maxillovomerine notch absent). *N. magister, albigula, mexicana, lepida, stephensi, fuscipes,* and *cinerea* all have the septum separated from the anterior palatal spine by a maxillovomerine notch. *N. albigula albigula* has a long, wide maxillovomerine notch which is truncated anteriorly. *N. a. laplataensis* and *N. a. brevicauda* have a smaller notch which is rounded anteriorly. *N. a. warreni* has a narrower notch tapering to a point, usually not reaching so far forward as in the other three subspecies. The condition of the septum in *N. a. warreni* thus approaches the condition (maxillovomerine notch absent) in the sympatric species *N. micropus canescens.*

The anterior palatal spine arises from the anterior margin of the palatal bridge and projects forward between the incisive foramina, usually extending about one third to one half the length of the incisive foramina. The base of the spine may continue onto the palatal bridge as a median crest. The spine may be relatively short and stout with a blunt tip, as in *N. lepida,* or may be longer and tapered to a thin point. The anterior palatal spine is formed by slender extensions of the right and left maxillaries fused in the median plane. The right and left sides of the palatal spine may be more or less incompletely fused, in which case a line or groove of contact remains visible on the median ventral edge of the spine. Such is the condition usually present in *N. mexicana inopinata,* and less distinctly seen in some individuals of *N. mexicana fallax* and *N. mexicana*

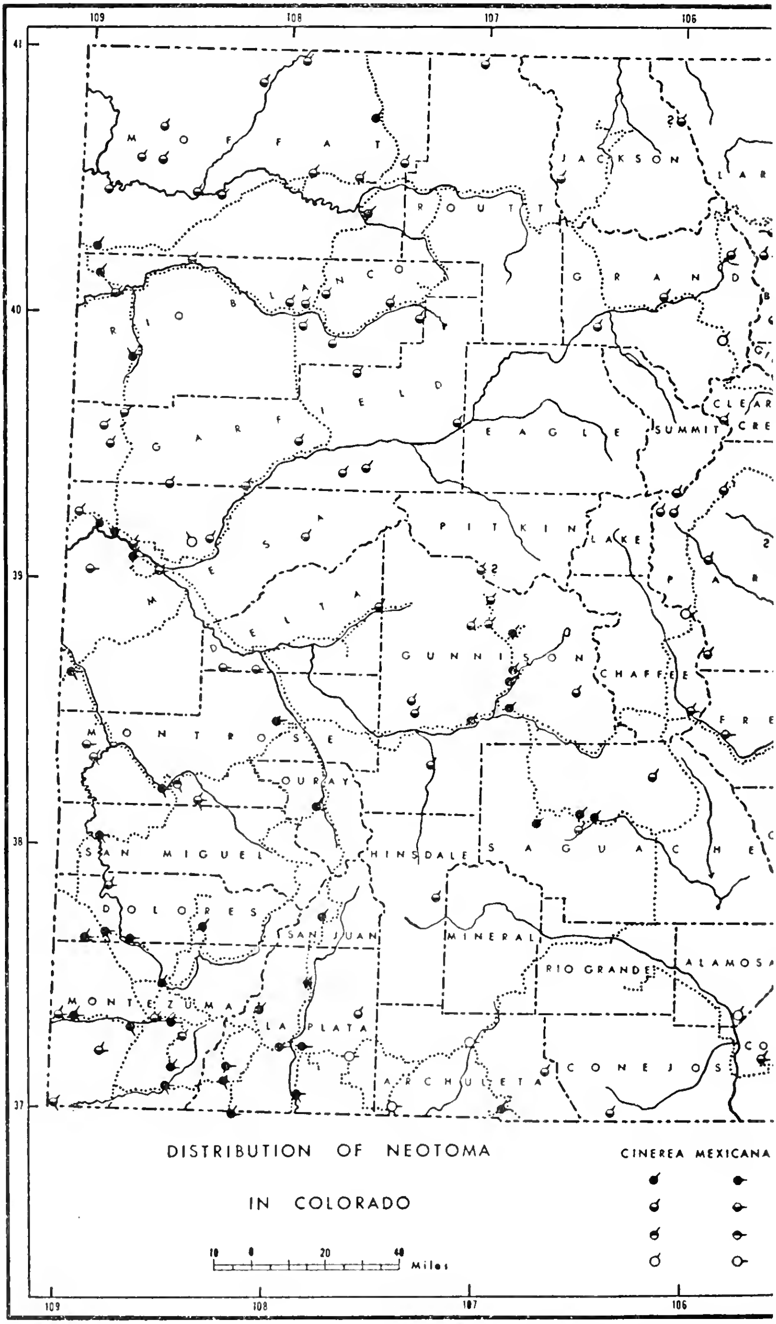
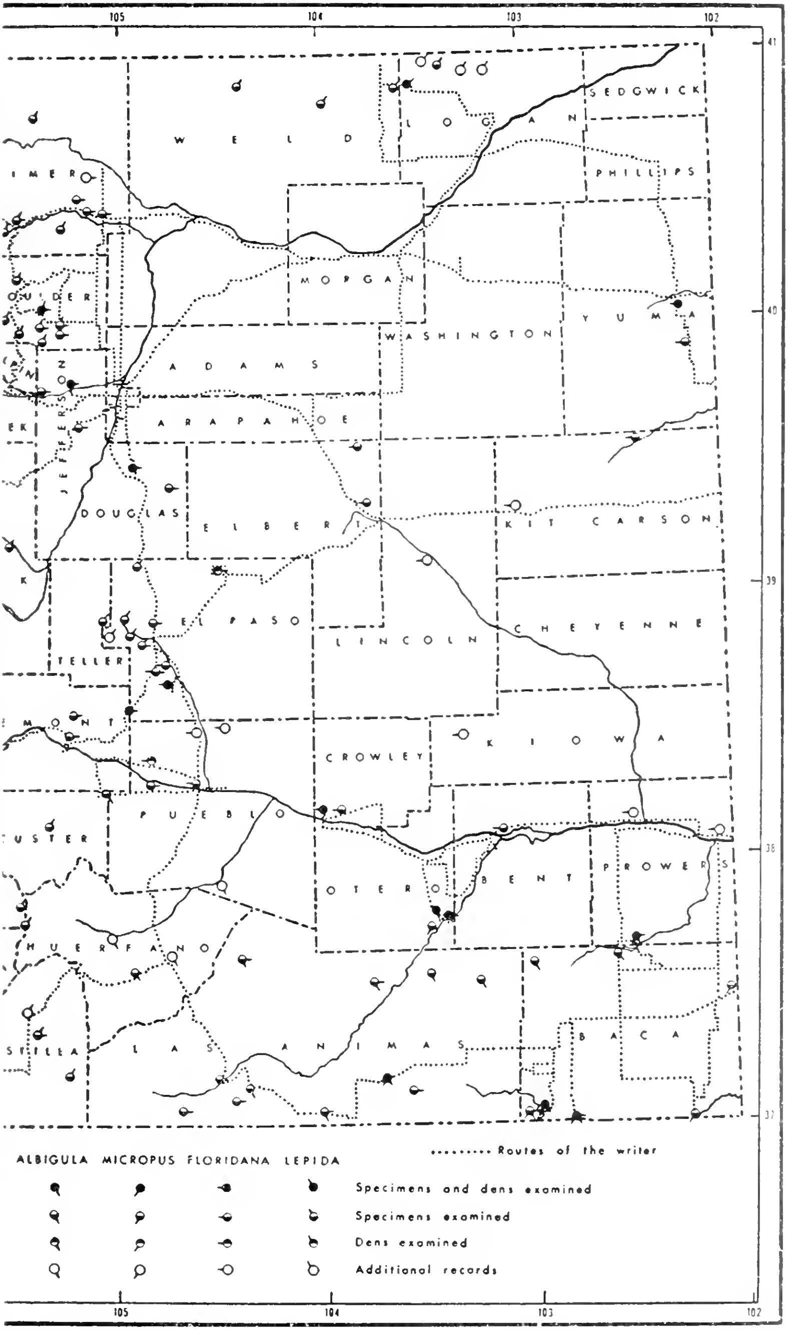


FIG. 1. Distribution of



wood rats in Colorado.

scopulorum. Most kinds of wood rats in Colorado have the anterior palatal spine completely fused and the median line obliterated in adults.

In contrast to the usual single-tipped condition, the anterior end of the palatal spine may be forked or Y-shaped, each prong tapering to a slender sharp tip over the middle of the right or left incisive foramen. The forked anterior palatal spine is a highly reliable specific character for *N. floridana.* It was present in all specimens of the several subspecies examined. No other species north of Mexico is characterized by a forked palatal spine, but occasional individuals of some species have a minutely double pointed tip, usually noticeable only under magnification. Only a single specimen was found (*N. albigula warreni*) with the anterior palatal spine as strongly forked as is usual for *N. floridana campestris.*

The cranial ridges of the occipital region of the skull ordinarily vary considerably with age and sex in wood rats and are of little taxonomic value. The presence or absence of an external occipital tubercle at the midpoint of the lambdoidal crest, however, is a constant, even if slight, difference. The tubercle is almost always present as a small distinct point in *N. micropus canescens,* but is absent in *N. albigula warreni.* The relative prominence of the lambdoidal crest and the external occipital crest varies in different populations of *N. albigula* and probably in other species.

Baculum

There is no doubt that the baculum of wood rats shows distinctive morphological characters on the specific level, and perhaps also on the subspecific level. Burt and Barkalow (1942: 287) have described and illustrated the bacula of many kinds of wood rats. I have found the baculum helpful in distinguishing *N. micropus canescens* from *N. albigula warreni.* I have not, however, mounted and described the bacula of other kinds of wood rats in Colorado, which are all recognizable without difficulty by features of the skin and skull.

SYSTEMATIC ACCOUNTS OF SPECIES AND SUBSPECIES

KEY TO THE SUBSPECIES OF NEOTOMA IN COLORADO

- 1. Tail bushy (tufted in young), sole of hind foot furred from heel to plantar tubercle . . . . (*cinerea*)
  - 2. Upper parts dark orange-buff with heavy overlay of black, bullae elongate and narrow . . . . *c. orolestes*, p. 256
  - 2′. Upper parts light orange-buff with light overlay of black, bullae round and inflated.
    - 3. Temporal ridges strong and angular, interparietal between temporal ridges only slightly wider than long . . *c. rupicola*, p. 270
    - 3′. Temporal ridges weak and flaring, interparietal between temporal ridges 1½ to 2 times wider than long . . . . *c. arizonae*, p. 260
- 1′. Tail not bushy, sole of hind foot naked to heel.
  - 4. Tail long-haired or slightly bushy, nearly unicolor . . *stephensi relicta* (may occur south of San Juan River in Montezuma County)
  - 4′. Tail short-haired, sharply bicolor.
    - 5. Breast fur mostly gray at base and with not more than a small patch of fur white to base, upper incisors slender.
      - 6. Spot of fur on breast white to base, anterior palatal spine stout and blunt . . . . *l. sanrafaeli*, p. 320
      - 6′. No fur on breast white to base, anterior palatal spine with thin sharp tip . . . . (*mexicana*)
        - 7. Skull strongly arched at base of rostrum, interorbital constriction near middle of frontal . . . . *m. scopulorum*, p. 278
        - 7′. Skull not strongly arched at base of rostrum, interorbital constriction more anterior.
          - 8. Frontal wide posteriorly, upper incisors yellow, *m. fallax*, p. 274
          - 8′. Frontal not so wide posteriorly, upper incisors deeper yellow-orange . . . . *m. inopinata*, p. 284
    - 5′. Breast almost entirely white to base of fur, upper incisors stout.
      - 9. Dark line around mouth . . . . *m. scopulorum*, p. 278
      - 9′. No dark line around mouth.
        - 10. Tail light gray above, anterior palatal spine forked, *f. campestris*, p. 316
        - 10′. Tail dark gray or black above, anterior palatal spine single-tipped . . . . (*albigula*)
          - 11. Upper parts bluish gray, nasal septum intact, *m. canescens*, p. 310
          - 11′. Upper parts bluish gray to grayish brown, nasal septum divided by maxillovomerine notch.
            - 12. Upper parts bluish gray with brownish or pinkish tinge on sides, temporal ridges strong and angular . . . . *a. warreni*, p. 297
            - 12′. Upper parts grayish brown, temporal ridges weak and smoothly flaring.
              - 13. Skull evenly arched, squamosal root of zygomatic arch forming a nearly right angle . . . . *a. brevicauda*, p. 291
              - 13′. Frontonasal region less arched than braincase, squamosal root of zygomatic arch forming an oblique angle, *a. laplataensis*, p. 293

KEY TO THE SUBSPECIES OF NEOTOMA IN COLORADO, USING SKULLS ONLY

1. Nasal septum intact, skull strongly arched in interorbital region.
    2. Anterior palatal spine forked, sphenopalatine vacuities narrow slits . . . . *f. campestris*, p. 316
    2′. Anterior palatal spine single-tipped, sphenopalatine vacuities wide . . . . *m. canescens*, p. 310

1′. Nasal septum divided by maxillovomerine notch, skull not strongly arched in interorbital region.
    3. Interpterygoid fossa narrow, sharply bounded laterally by straight angular rims on palatines.
        4. Anterior palatal spine stout and blunt, rostrum short and slender, basilar length less than 35 mm . . . . *l. sanrafaeli*, p. 320
        4′. Anterior palatal spine slender and pointed, rostum long to medium, basilar length 35 mm or more . . . . *(cinerea)*
            5. Temporal ridges strong and angular, interparietal between temporal ridges only slightly wider than long.
                6. Upper incisors large, bullae round and inflated, *c. rupicola*, p. 270
                6′. Upper incisors medium, bullae elongate and narrow, *c. orolestes*, p. 256
            5′. Temporal ridges weak and flaring, interparietal between temporal ridges 1½ to 2 times wider than long, upper incisors small . . . . *c. arizonae*, p. 260
    3′. Interpterygoid fossa rounded, not sharply bounded laterally by straight angular rims on palatines.
        7. Upper incisors small, diastema usually shorter than 10.6 mm, *stephensi relicta* (may occur south of San Juan River in Montezuma County).
        7′. Upper incisors medium to large, diastema usually longer than 10.6 mm.
            8. Anterointernal fold of first upper molar deep, upper incisors slender.
                9. Temporal ridges prominent, recurving with abrupt angle on parietals . . . . *a. warreni*, p. 297
                9′. Temporal ridges less prominent, smoothly flaring on parietals . . . . *(mexicana)*
                    10. Skull strongly arched at base of rostrum, interorbital constriction near middle of frontal, *m. scopulorum*, p. 278
                    10′. Skull not strongly arched at base of rostrum, interorbital constriction more anterior.
                        11. Frontal wide posteriorly, upper incisors yellow, *m. fallax*, p. 274
                        11′. Frontal not so wide posteriorly, upper incisors deeper yellow-orange . . . . *m. inopinata*, p. 284
            8′. Anterointernal fold of first upper molar shallow, upper incisors stout.

12\. Interorbital constriction near middle of frontal . . . *m. scopulorum,* p. 278
12′. Interorbital constriction more anterior . . . . (*albigula*)
  13\. Temporal ridges strong and angular, skull moderately arched in frontonasal region . . . . *a. warreni,* p. 297
  13′. Temporal ridges weak and smoothly flaring, skull only slightly arched.
    14\. Skull evenly arched, squamosal root of zygomatic arch forming a nearly right angle . . . . *a. brevicauda,* p. 291
    14′. Frontonasal region less arched than braincase, squamosal root of zygomatic arch forming an oblique angle,
a. laplataensis, p. 293

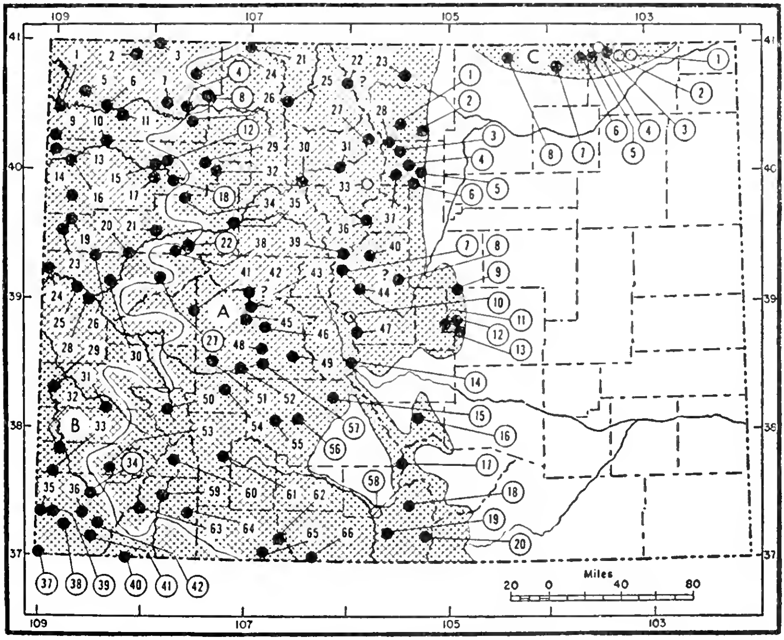
Neotoma cinerea (Ord)

Bushy-tailed wood rat

Mus cinereus Ord, *in* Guthrie, A new geographical, historical, and commercial grammar; . . . Edit. 2, vol. 2, p. 292, Philadelphia, 1815.

Neotoma cinerea, Baird, Mammals: General report upon the zoology of the several Pacific Railroad routes. *In* Reports, explorations, and surveys for a railroad route from the Mississippi River to the Pacific Ocean, vol. 8, pt. 1, p. 499, 14 July 1858.

Distribution.—Cordilleran Region from southern Yukon southeast to northern New Mexico and Arizona, and from the Black Hills of South Dakota west



NEOTOMA CINEREA

FIG. 2. Distribution of *Neotoma cinerea* in Colorado. Ranges of subspecies: A, *N. c. orolestes;* B, *N. c. arizonae;* C, *N. c. rupicola.* Symbols: solid circles, specimens examined; hollow circles, additional records. Numbers refer to localities listed under subspecies accounts (see pp. 259, 270, and 273).

to the Pacific Ocean, along the Pacific Coast south into northern California, thence inland through the Sierra Nevada. In Colorado the species occurs in all parts of the state west of the Great Plains.

Diagnosis.—Size large; hind feet and ears large; tail bushy; sole of hind foot furred from heel to posterior tubercle. Skull long and angular; rostrum long and narrow; frontal region narrowly constricted and channeled; temporal ridges usually prominent, narrowly or moderately diverging posteriorly, and turning abruptly inward at line of widest separation on or close to anterior edge of interparietal; incisive foramina long and narrow, ends slightly tapered or rounded; interpterygoid fossa usually narrow and sharply bounded laterally by angular ridges on palatines; bullae large.

Comparisons.—*Neotoma cinerea* differs from other species of wood rats in a number of important characters which usually have been regarded as justifying the recognition of a separate subgenus, *Teonoma* Gray, for *Neotoma cinerea.* It differs from all other species of wood rats known from Colorado as follows; ears larger; tail bushy; sole of hind foot fully furred from heel to proximal tubercle; interorbital region narrowly constricted and channeled; frontal and temporal ridges narrowly separated. For additional differences see accounts of other species.

Neotoma **cinerea orolestes** Merriam

Neotoma orolestes Merriam, Proc. Biol. Soc. Washington, 9: 128, 2 July 1894.

Neotoma cinerea orolestes, Warren, Colorado Coll. Publ., Gen. Ser. no. 19, p. 248, January 1906; Goldman, N. Amer. Fauna 31: 104, 19 October 1910, part; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 116, 1910; Cary, N. Amer. Fauna, 33: 111, 17 August 1911; Hooper, Univ. California Publ. Zool., 42; 422, 17 May 1940; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 217, 1942.

Neotoma cinereus [sic], Allen, Bull. Essex Inst., 6: 56, April 1874.

Neotoma cinerea, Coues and Yarrow, Report U. S. Geol. and Geog. Explor. and Surv. West 100th Merid., 5: 101, Sept. 1876.

Type.—USNM (BSC) no. 35906/48215, adult male, skin and skull; from Saguache Valley, twenty miles west of Saguache, Saguache County, Colorado; collected 13 August 1892 by J. Alden Loring.

Range.—Outside of Colorado, the subspecies occurs in the Rocky Mountains from southern Montana south into north central New Mexico. It ranges west to the Yellowstone National Park and east into the Black Hills, South Dakota. In Colorado, it occupies all of the central mountainous part of the state from the foothills of the Front Range, Pikes Peak, and the Culebra Range westward to the western slopes of the White River Plateau, Grand Mesa, and the La Plata Mountains. *N. c. orolestes* has a much more extensive range in Colorado than any other subspecies of wood rat. (See map, Fig. 2.)

Diagnosis.—Upper parts orange buff to pinkish buff and heavily overlaid with black; sides of belly nearly to median line with fur basally gray and distally white or light colored; rostrum long; nasals somewhat spatulate anteriorly;

frontonasal region strongly ridged and channeled; temporal ridges usually narrowly separated; sphenopalatine vacuities large.

Description.—Adults in fresh pelage taken in January, at Crested Butte, Colorado: size large; tail about 76 per cent as long as head and body; hind feet large. Pelage: long and dense; tail bushy and distichous, maximum length of lateral hairs 40 mm; longest vibrissae 94 mm. Color: upper parts Inca Gold, 11 J 7, to orange buff, 11 F 7 (R: Ochraceous Buff to Cinnamon Buff), heavily overlaid with blackish; sides and cheeks lighter and brighter (M and P: near Mellow Gold, 10 H 6; R: Light Ochraceous Buff); top of muzzle grayer; underparts white, fur gray basally except on throat and breast where white to base, but short hair over mid-ventral glandular area of skin in males usually buffy or drab; tail bicolor, gray above with ochraceous tinge on proximal third, white below with buffy basal band; feet white.

Skull: large and prominently ridged; rostrum long; zygomatic arches rounded and converging anteriorly, robust; nasals widely rounded anteriorly, slightly spatulate in dorsal view, tapering evenly posteriorly to rounded or ragged ends; premaxillary extensions posterior to nasals long and slender; frontonasal region slightly arched and strongly channeled; interorbital ridges sharp posteriorly; temporal ridges nearly straight, not widely separated, angular rather than smoothly flaring posteriorly; interparietal nearly as long as width between temporal ridges; incisive foramina long, nearly paralled-sided and ends nearly equally rounded; anterior palatal spine tapered to thin narrow blade or point touching vomer; septum deeply notched between palatal spine and vomer; posterior edge of palate usually convex, sometimes square or pointed; interpterygoid fossa narrow, bounded laterally by straight, nearly parallel angular ridges on palatines; sphenopalatine vacuities long and wide; auditory bullae elongate on diagonal axes converging anteriorly; incisors moderately slender; upper molars moderate in size; anterointernal fold of M1 cutting at least half way across enamel loop.

Adults in worn pelage taken in July, 3 mi. N Almont: pelage short and rough; tail less bushy than in adults taken in January; color of upper parts duller, more grayish; some individuals more salmon or pinkish on sides; whitish hair tips of under parts shorter, allowing more basal coloration to show through.

An immature taken in June at Crested Butte: total length 255 mm; tail 100 mm; hind foot 36 mm; full juvenal pelage soft, fine and fluffy; upper parts darker and grayer than in adults; tail light gray, becoming whitish distally, covered with short fuzzy hairs forming a tufted, not bushy, tip; ears fringed with whitish.

Comparisons.—N. c. orolestes differs from *N. c. arizonae* and *N. c. rupicola* in darker color, longer hind foot, longer rostrum, more spatulate nasals, less inflated bullae, more prominent and less widely separated temporal ridges, and usually larger size. From *N. c. cinerea* to the north, *orolestes* differs in wider sphenopalatine vacuities and usually more buffy (less gray) upper parts. From *N. c. alticola* and *N. c. acraia* to the northwest and west, *orolestes* differs in presence of sphenopalatine vacuities, smaller upper incisors, and usually more intense coloration of upper parts.

Remarks.—Comparison of 35 specimens of all ages and seasons from northern Gunnison County, with the type and five near topotypes from Saguache County, reveals no geographic variation. Because the series from Gunnison County is more nearly adequate than any other, it was used as a basis for the description and comparison. *N. c. orolestes* is highly variable in color, size, and cranial characters. Much of this variation is individual and but little of it geographic.

In series of adults from several localities in Colorado, young adults are more yellowish on the back and sides, and the older ones are more pinkish. An old adult female (KU 34836) from eight miles north and one mile west of Hesperus, taken 5 July 1949, has a more reddish hue than any of comparable age, being Rose Dawn, 3 B 9 (R: Buff-Pink), on the sides.

Four adults from Grand Lake and five from Sulphur Springs taken in April and May are brighter orange than comparable specimens from Crested Butte. Four adults taken in March and April from the Sangre de Cristo Range, 24 miles east of Hooper, 8500 feet, are somewhat lighter than adults from Gunnison County but show no constant cranial differences.

Specimens from 16 miles north of Craig show intergradation with *N. c. arizonae* in lighter color, narrower rostrum, and wider interparietal between temporal ridges. In other characters they most resemble *orolestes,* to which they are here referred. One of these has a total length of 425 mm and is the largest wood rat I have seen from Colorado. A young adult is unusually reddish, near Rose Dawn, 3 B 9 (R: Buff-Pink), on the hips. Specimens from Three Forks, Routt County, are intergrades between *N. c. orolestes* and *N. c. arizonae.* Although the adults are still too young to show distinctive subspecific cranial characters, they are assigned to *N. c. orolestes.*

Three specimens from nine miles northeast of Buford show intergradation between *N. c. arizonae* and *N. c. orolestes* but are referable to the latter. Two adults from the P. Slideler Ranch, Middle Mamm Creek, south of Rifle, taken in July and August are intergrades. They are closer to *arizonae* in color, but closer to *orolestes* in cranial characters, and are here referred to *orolestes.* Two young adults from one mile northeast of Bowie show some intergradation with *arizonae* in a few cranial characters. Four adults from Vallecito Camp, taken in June and July, show intergradation with *arizonae* in color and width of separation of the temporal ridges. The bullae are round and inflated as in *arizonae.* Other characters are as in *orolestes,* to which the specimens are referred. Two adults from 10 miles east and 15 miles north of Dolores resemble *orolestes* in most characters but show intergradation with *arizonae* in color, size of incisors and rostrum, and shape of nasals.

An adult female of the year (DMNH 2349) from Jefferson, taken in September, is starting to molt on the venter and sides and has a white diamond-shaped splotch 28 mm long and 14 mm wide on the nape. A small white spot on the nape is present in six specimens as follows: subadult male from Hoosier Pass; subadult female from Lake Moraine; two subadult males from nine miles northeast of Buford; subadult female from the head of the Navajo River; adult male from six and one half miles southwest of Silverton. In each specimen the hairs are white to the base and the white spots resemble those on some *N. c. arizonae* (see p. 269).

An adult male (KU 34831) from six and one half miles southwest of Silverton, altitude 10,100 feet, has, in addition to the white spot described above, a deformed skull. The rostrum and incisive foramina are bent slightly to the right. The skull shows no evidence of mechanical injury. In addition, the same skull has each maxillary abnormally divided by a suture on the lower side of the rostrum, from the ventral edge of the antorbital foramen across the root of the incisor. Another specimen (KU 34834 ♀), from 8 miles north and 1 mile west of Hesperus, has a similar suture on the right maxillary crossing the root of the incisor but no such suture on the left maxillary.

Specimens examined.—Total 261, from Colorado as follows: (*1*) Estes Park, 18 (9 BSC, 1 USNM, 8 AMNH); (*1*) 4 mi. SW Estes Park, 1; (2) Pinewood, 2 (AMNH); (*3*) 12½ mi. S Estes Park, 8400 ft., 1; (*4*) Gold Hill, 6 (BSC): (5) Boulder, 5 (CNHM); (5) S of Boulder, 1 (UCM); (5) Marchioness Tunnel W of Boulder, 1 (UCM); (5) E face Green Mt. near Boulder, 1 (UCM); (5) Gregory Canyon, 6000 ft., 2 (UCM); (6) 3 mi. E. Pinecliffe, Boulder Co., 2 (DMNH); (*unlocated*) Bluebird, Boulder Co., 1 (UCM); (7) Alma, 1 (DMNH); (7) Buckskin Cr., 1 mi. above Alma, 1 (ERW); (7) Mosquito Gulch, 10,500 ft., 1 (ERW); (*8*) Tarryall Creek Camp, 8700 ft., "6 mi. above Puma City" (E. R. Warren catalog), 1 (ERW); (*9*) Palmer Lake, El Paso Co., 1 (DMNH); (*11*) Glen Cove, Pikes Peak, Teller Co., 3 (MZ); (*11*) Lake Moraine, 10,250 ft., El Paso Co., 8 (5 ERW, 2 AMNH, 1 MVZ); (*12*) Cascade, 1 (BSC); (*12*) Minnehaha, 8400 ft. [38° 51′ N, 104° 57′ W], 5 (MZ); (*13*) Colorado Springs, 1 (ERW); (*13*) Bear Creek Cañon, 7100 ft., opposite Palmer Rd., Colorado Springs, 1 (ERW); (*13*) Bear Creek, 8300 ft., 1 (ERW); (*13*) Hunter's Cr., tributary of Bear Cr., 7500 ft., 1 (ERW); (*14*) Salida, 2 (1 ERW, 1 UCM); (*15*) Bonanza, 1 (DMNH); (*16*) Querida, 9000 ft., 4 (ERW); (*17*) Madenos Cañon [=Medano Cr. ?], above Herard's, 8700 ft., Saguache Co., 1 (ERW); (*17*) 24 mi. E Hooper, 8500 ft., Sangre de Cristo Range, 4 (DMNH); (*18*) 5 mi. SSE Garland, 1 (AMNH); (*19*) 3 mi. W San Acacio, 8050 ft., 2; (*20*) Culebra Canyon, 9400 to 9100 ft., 4 (ERW); (*21*) Three Forks, 30 mi. above Baggs Crossing, 3 (AMNH); (*unspecified*) Routt Co., 1 (DMNH); (22) Medicine Bow Range, 1 (DMNH); (23) 2 mi. E Log Cabin (and 6 mi. E Elkhorn), 7450 ft., 1 (ERW); (*unspecified*) Larimer Co., 1 (DMNH); (*24*) 16 mi. N. Craig, 6600 ft., 5; (*25*) Buffalo Pass Sawmill, 8880 ft., Jackson Co., 1 (ERW); (*26*) 4 mi. W and 8 mi. S Craig, 6400 ft., 1; (*27*) Grand Lake, 8300 ft., 5 (3 ERW, 2 DMNH); (*28*) Longs Peak, 1 (BSC); (*28*) Ft. Mount Meeker, 8700 ft., Boulder Co., 4 (AMNH); (*29*) 9 mi. NE Buford, Lost Creek, 3 (CM); (*30*) Camp near Sheephorn Pass, 8200 ft., Grand Co., 1 (ERW); (*31*) [Hot] Sulphur Springs, "taken at 7800 ft. or more" (E. R. Warren catalog), 5 (ERW); (*32*) Marvine Mts., Rio Blanco Co., 1 (USNM); (*unlocated*) Compass Creek, 9000 ft., Rio Blanco Co., 3 (AMNH); (*34*) E. Fork Rifle Creek (20 mi. NE Rifle), 2 (BSC); (*35*) 12 mi. above Glenwood Springs, 6000 ft., Grand River Canyon, Garfield Co., 2 (ERW); (*36*) Grays Peak, 2; (*37*) Nederland, 1 (CNHM); (*37*) Silver Lake Mine, 10,000 ft., 3 (2 CNHM, 1 USNM); (*37*) 3 mi. S Ward, 9000 ft., 3; (*37*) ½ mi. E and 3 mi. S Ward, 9400 ft., 7; (*unspecified*) Boulder Co., 9 (USNM); (*38*) P. Slideler Ranch, near Rifle, Middle Mamm Cr., 2 (DMNH); (*39*) Summit of Hoosier Pass, 1 (DMNH); (*40*) Jefferson, 2 (DMNH); (*unlocated*) Williams Ranch, Park Co., 1 (DMNH); (*41*) 1 mi. NE Bowie, 6300 ft., Delta Co., 1; (*42*) Elk Mountains, 1 (USNM); (*43*) Gothic, Sylvanite Mine, 12,000 ft., 3 (ANSP); (*44*) Garo, Trout Cr. Ranch, 9500 ft., 2 (BSC); (*45*) Crested Butte, Decker's Ranch, 9000 ft., 10 (9 ERW, 1 AMNH); (*45*) Irwin, 10,700 ft., Hallowell's Camp, in Upper Venango Tunnel, 4 (3 ERW, 1 AMNH); (*46*) 3 mi. S and 6½ mi. E Crested Butte, 9200 ft., 7; (*46*) 2 mi. S and 9 mi. E Crested Butte, 9400 ft., 2; (*47*) Head of Badger Creek, "Chaffee Co." [?, probably Park Co.], 2 (ERW); (*48*) Almont, 2 (BSC); (*48*) 3 mi. N Almont, 8300 ft., 9; (*48*) 1 mi. SW Almont, 8000 ft., 1; (*49*) 5 mi. NE Ohio [38° 37′ N, 106° 32′ W], 1 (UCM); (*50*) 2 mi. NE Ridgway, 7200 ft., 1; (*51*) near Forest Reserve Camp, sec. 7, T. 49 N, R. 4 W, 8250 ft., 1 (ERW); (*51*) Divide between Sapinero and Currecanti creeks, 9350 ft., 1 (ERW); (*52*) 6 mi. W and 3 mi. S Gunnison, 7600 ft., 2; (*53*) 10 mi. E and 15 mi. N Dolores, 8250 ft., 2; (*54*) Dayton [38° 21′ N, 107° 13′ W], 1 (USNM); (*55*) 32 mi. W and 2 mi. N Saguache, 9800 ft., 1; (*56*) 20 mi. W Saguache, 1 (BSC); (*56*) 22 mi. W Saguache, 14 (MVZ); (*56*) 20 mi. W and 3 mi. N Saguache, 9000 ft., 1; (*56*) 17 mi. W and 4 mi. N Saguache, 8500 ft., 1; (*56*) 21½ mi. W and 4½ mi. N Saguache, 9300 ft., 1; (*56*) Tevebaugh's Ranch (20 mi. W Saguache and 9 mi. S Cochetopa Pass, 2 (BSC); (*57*) 3 mi. E Gunnison, 7900 ft., 1; (*59*) 1 mi. E and 7 mi. N Hermosa, 8100 ft., 1; (*60*) 6½ mi. SW Silverton, 10,100 ft., 1; (*61*) Hermit [approximately 37° 48′ N, 107° 13′ W], Hinsdale Co., 1 (BSC); (*62*) Headwaters of Navajo River, Archuleta Co., 7 (DMNH); (*63*) 8 mi. N and 1 mi. W Hesperus, 9500 ft., 4; (*64*) Vallecito Camp, "21 mi. N Bayfield" [probably by road; by air, 11 mi. N and 1 mi. E Bayfield], 7400 ft., 4 (AMNH); (*65*) Chromo, 3 (DMNH); (*65*) 2 mi. W and 1 mi. S Chromo, 7200 ft., 1; (*66*) Osier, Conejos Co., 6 (DMNH).

Additional records.—(*10*) 8½ mi. NE Buena Vista, 8750 ft., Chaffee Co. (4 TCWU, not seen); (*11*) Pikes Peak, 14,110 ft., El Paso Co. (Warren, 1942: 217); (*18*) Fort Garland (Coues and Yarrow, 1875: 102); (*33*) near Fraser (Cary, 1911: 111); (*36*) Mt. McClellan, timber line, Clear Creek Co. (Cary, 1911: 113); (*58*) Rio Grande, Alamosa Co. (Coues and Yarrow, 1875: 102).

Neotoma cinerea arizonae Merriam

Neotoma arizonae Merriam, Proc. Biol. Soc. Washington, 8: 110, 31 July 1893; Warren, Colorado Coll. Publ., Gen. Ser. no. 33, p. 75, January 1908; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 120, 1910.

Neotoma cinerea arizonae, Goldman, N. Amer. Fauna, 31: 106, 19 October 1910; Cary, N. Amer. Fauna, 33: 113, 17 August 1911; Hooper, Univ. California Publ. Zool., 42: 422, 17 May 1940; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 219, 1942.

Neotoma cinnamomea Allen, Bull. Amer. Mus. Nat. Hist., 7: 331, 8 November 1895; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 120, 1910.

Neotoma cinerea orolestes, Goldman, N. Amer. Fauna, 31: 105, 19 October 1910, part; Cary, N. Amer. Fauna, 33: 111, 17 August 1911, part; Hooper, Univ. California Publ. Zool., 42: 422, 17 May 1940, part.

Neotoma cinerea cinnamomea, Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 221, 1942; Hooper, Jour. Mamm., 25: 415, 12 December 1944.

Type.—USNM no. 186482, adult female, skin and skull; from Keams Cañon [=Keam Canyon], Navajo County, Arizona; collected 21 May 1888 by J. Sullivan.

Range.—The subspecies, as understood by me, ranges from southwestern Wyoming south through the semiarid canyon country of eastern Utah and Colorado as far as the Mogollon Rim in Arizona and New Mexico. In Colorado the subspecies occurs from the northern to the southern border of the state west of the high mountains and Grand Mesa. (See map, Fig. 2.)

Diagnosis.—Upper parts pale ochraceous or pinkish buff to pale buff, lightly to moderately overlaid with blackish; tail light gray above, some specimens with whitish fringe distally; buffy band below on base of tail; skull usually small, smooth, and light for the species; rostrum slender; nasals relatively narrow anteriorly (not spatulate); temporal ridges usually widely separated; interparietal between temporal ridges noticeably wider than long; sphenopalatine vacuities long and wide; bullae inflated ventrally; upper incisors slender.

Description.—Adults in slightly worn pelage taken in April at Cortez: size small to medium; tail about 76 per cent as long as head and body; hind foot of medium length; ears large. Pelage: short to medium in length, moderately dense to thin; tail slightly bushy and distichous, maximum length of lateral hairs 34 mm; longest vibrissae 92 mm. Color: upper parts light orange buff (M and P: Sweetmeat, 11 C 5, to 11 F 6; R: Pinkish Buff to Light Ochraceous-Buff) moderately overlaid with black; sides and forelegs brighter, near Cornhusk, 10 E 5 (R: Pale Yellow-Orange); ears dark grayish brown, borders faintly fringed with buff; throat, breast, and usually median ventral line white to base of hairs; sides of belly with hairs gray basally and white distally; tail bicolor, light gray above, pure white below, the white hairs visible from above as whitish fringe around tip of tail; buffy or pinkish buff band under base of tail; feet white.

Skull: usually small, smooth, and lightly constructed for the species; rostrum short and slender; zygomatic arches narrow, smoothly rounded anteriorly; nasals relatively narrow anteriorly, lateral borders nearly straight, converging posteriorly to irregular or ragged ends; premaxillary extensions posterior to nasals short to long; frontonasal region slightly arched and channeled; temporal ridges weak, usually widely separated for the species, variably curved or straight; interparietal between temporal ridges wider than long; incisive foramina narrow, slightly spindle-shaped; anterior palatal spine tapered to thin point touching vomer; septum deeply notched between palatal spine and vomer; posterior edge of palate variable, concave to pointed; interpterygoid fossa narrow or wide for the species, bounded laterally by curving ridges on palatines; sphenopalatine vacuities long and wide; auditory bullae rounded and inflated ventrally; incisors slender; upper molars relatively large; anterointernal fold of M1 deep or shallow.

Adults in worn pelage taken in early August, 4 mi. W and 2 mi. S Cahone, Colorado: pelage short and mostly thin; color duller, more grayish than in adults from Cortez taken in April; black overlay on back nearly the same.

A subadult taken in July at Four Corners: total length 295 mm; tail 132 mm; molt to subadult pelage not completed; dense subadult pelage on sides and rump; thin juvenal pelage on back; tail slightly bushy, except extreme tip of soft fine juvenal hairs. Color: subadult pelage on sides and rump lighter buff, less vivid (M and P: near Leghorn, 10 D 4; R: near Light Buff, XV 17′ e) than in adults; juvenal pelage on back grayer but not darker than mature pelage in adults; tail bicolor, gray above with whitish fringe on tip, white below with narrow light buff basal band. (This specimen, the best subadult at hand from Montezuma County, seems to be abnormally small for a wood rat of its age, as indicated by pelage and tooth wear. Another anomaly is that all hairs of the subadult pelage at the molt line are of full length; none is short, in process of growing in underneath the old juvenal pelage. The molt seems to have stopped on the back without progressing to completion. However, there seems to be no reason to regard the colors as abnormal.)

An immature taken in July, 4 mi. W and 2 mi. S Cahone: total length 274 mm; tail 115 mm; juvenal pelage full grown, thin, soft and fluffy; tail tufted, not bushy, basal half with short fuzzy hairs, hairs on distal half becoming longer and straighter toward tip. Color: upper parts grayer but no darker than in adults; faint buffy wash on sides and shoulders, becoming brightest (M and P: near Sunset, 10 D 5; R: Pale Yellow-Orange) on forelegs and cheeks; small white spot below base of each ear; tail bicolor, light gray above except for longer ivory-colored hairs on distal half, white below with faint diffuse buffy basal band.

A juvenile taken in May at Four Corners: total length (dry skin) 126 mm; tail (dry skin) 46 mm; eyes closed; juvenal pelage not yet full length, hairs very short and straight; colors same as in adult, except that black-tipped overhairs on back are so short and closely spaced as to give middorsal region a nearly black appearance almost concealing buffy underfur; ears furred, blackish on upper outer surface, whitish over entire inner surface; tail thinly covered with very short fine hairs, slightly bicolor.

Comparisons.—*N. c. arizonae* differs from *N. c. orolestes* as follows: size averaging smaller; color of upper parts lighter, usually richer; fur on belly usually with less extensive basal gray coloraton; tail less bushy; skull smoother, more lightly built; incisors more slender; rostrum smaller and zygomatic arches narrower relative to basilar length; nasals narrower anteriorly; bullae more rounded and inflated ventrally; frontal region less channeled; temporal ridges weaker, usually more widely separated on parietals; interparietal between temporal ridges wider and shorter (not so squarish); sphenopalatine vacuities usually somewhat wider.

Color is not a reliable basis for separating *N. c. arizonae* from *N. c. rupicola* in Colorado, although topotypes of *rupicola* are slightly lighter than any of the specimens from Colorado that I have seen of either subspecies. In *rupicola* from Colorado the average extent of the gray basal coloration of the belly fur is less than in *arizonae*. However, numerous specimens of either subspecies from various localities in Colorado, Nebraska, Wyoming, Utah and Arizona are indistinguishable on the basis of color. In cranial characters *arizonae* differs from *rupicola* as follows: upper incisors markedly smaller; rostrum more slender; sphenopalatine vacuities wider; nasals usually narrower anteriorly; interpterygoid fossa usually narrower; anterointernal fold of M1 usually shallower.

N. c. arizonae differs from *N. c. alticola* and *N. c. acraia* chiefly in presence of sphenopalatine vacuities, and lighter color.

Remarks.—From Montezuma County, the part of Colorado nearest to the type locality of *Neotoma cinerea arizonae*, 21 specimens (including 14 adults) were available to me. These were collected at ten localities between 4850 and 7000 feet elevation (see Fig. 2 and *specimens examined*). Study of these specimens revealed much variability but no geographic variation within the county. Five specimens from Arizona, of which three (including the holotype) are from Keam Canyon, one from Walpi, and one from Oraibi, were examined and measured. They fall within the range of variation of the series from Montezuma County in characters of the pelage and skull. Accordingly, the specimens from Montezuma County are here used as the basis for description and comparison of the subspecies.

Specimens of *N. c. arizonae* from western Dolores, Montrose, and Mesa counties do not differ significantly from those collected in Montezuma County. Among four adults from 4 miles west and 2 miles south of Cahone, 7000 feet, Dolores County, collected 1 to 5 August 1949, one (KU 34843 ♀, third year adult) has much more reddish upper parts than the other three, or indeed, than any other specimens of *arizonae* that I have seen. It is Salmon, 10 A 7 (R: Salmon Color) on the sides, in contrast to Cornhusk, 10 E 6 (R: near Pale Yellow-Orange, III 15 e), for the other three adults.

Nine specimens of *arizonae* from Grand Junction, Mesa County, collected in September and October, 1905, are all first year adults molting to first autumn and first winter pelages on the back and sides (see p. 402). They are darker than comparable specimens from Montezuma County, more nearly resembling in color *N. c. orolestes* of similar age. In small size the specimens from Grand Junction resemble *arizonae* from Montezuma County. The upper incisors average slightly wider in specimens from Grand Junction, but the skulls are, to me, otherwise indistinguishable. The nine specimens collected by E. R. Warren and labeled "Grand Junction, Colo." actually came from the west side of the Gunnison River southwest of Grand Junction (E. R. Warren, unpublished diary, 1905: 75). These specimens were referred to *orolestes* by Goldman (1910: 105) and Warren (1942: 217). They are intergrades and are here referred to *arizonae.*

Three specimens from one mile southwest of Fruita, on the north side of the Colorado River, are also intergrades between *arizonae* and *orolestes.* They are nearly as dark as comparable specimens of *orolestes* but smaller. The skulls of a first year adult female and a second year adult female do not differ from specimens of the same age and sex from Montezuma County. The skull of a second year adult male, however, differs from comparable skulls in greater length, longer nasals and rostrum, more channeled frontal region, stronger temporal ridges less widely separated, and narrower interparietal between temporal ridges, thus resembling *orolestes.* The skull resembles *arizonae* in narrow nasals and rostrum, slender upper incisors, inflated bullae, and shallow anterointernal fold of M1. The three specimens are referred to *arizonae.*

Two adults from eight miles west of Rifle agree with *arizonae* in size and color but resemble *orolestes* in length of rostrum, less arched skull, more channeled frontal region, and temporal ridges prominent and less widely separated. One skull has also more elongate bullae as in *orolestes;* the other has smaller rounded bullae. These two specimens are intergrades referrable to *arizonae.* An adult female from 12 miles southeast of Rifle is referrable to *arizonae* on the basis of pelage and most cranial characters but shows intergradation with *orolestes* in the less arched and more channeled frontonasal region and more elongate bullae. Of two specimens from 20 miles northeast of Rifle, the adult female shows intergradation between *arizonae* and *orolestes.* The skin is more like *arizonae,* but the skull resembles *orolestes* in the shape of the bullae and the flaring of the nasals anteriorly. The subadult male is too young to show clear characters of either race. The two specimens seem best referred to *arizonae.*

Twelve adults of *arizonae* from Rio Blanco County (localities *12, 13, 17,* and *18* of Fig. 2) are all in worn summer pelage and, in color, closely resemble comparable specimens from Montezuma County. In cranial characters many specimens from Rio Blanco County east of the 108th meridian show intergradation with *orolestes.* Specimens from five miles south of Meeker and from six miles northeast of Meeker differ from specimens from Montezuma County in wider upper incisors, smaller sphenopalatine vacuities, anteriorly wider nasals, and slightly larger rostrum. One adult male, among five specimens from six miles northeast of Meeker, is larger and has narrower and more prominent temporal ridges. Its skull resembles that of *orolestes* more than that of *arizonae* but the other four specimens from the same locality resemble *arizonae* more closely. All five specimens are referred to *arizonae*.

Twelve young and adult wood rats from Dry Fork, Rio Blanco County, taken in June, July, and November, when compared with those from Montezuma County, show a likeness which is remarkable, considering the marginal geographic position of Dry Fork far northeast for the subspecies. In pelage the wood rats from Dry Fork and Montezuma County are, to me, indistinguishable. Some adults from Dry Fork have slightly wider upper incisors. Only the skull of the largest specimen suggest intergradation between *arizonae* and *orolestes* in the shape of nasals, rostrum, and frontal region, and in the more elongate, less inflated bullae.

The 34 specimens examined from Moffat County show a wide range of variation in color, size, and cranial characters. Six adults from western Moffat County (localities *1*, *5*, and *11* of Fig. 2) are lighter with a lesser overlay of black and are slightly more buffy than adults from southwestern Colorado. This difference seems to be at least in part due to season, as all adults from Moffat County were collected in summer, in worn pelage. The skulls of the six adults resemble those from Montezuma County except for greater variation in shape of bullae, size of sphenopalatine vacuities, and width of upper incisors. Four subadults and one immature from localities *5* and *11* are not appreciably different in color from specimens of comparable age from southwestern Colorado.

The eight specimens at hand from Snake River (localities *2* and *3*) resemble *N. c. arizonae*, to which they are referred, but are more variable in color, size of upper incisors, shape of auditory bullae, and configuration of temporal ridges. These features suggest intergradation with *N. c. orolestes*. One adult from Snake River (AM 11436/9723) taken on 25 August 1895, has unusually long new pelage with as much black on the back as *orolestes*. An old adult from five miles west of Craig and a subadult from eight miles northeast of Craig are intergrades here referred to *arizonae* but which perhaps with equal propriety could be referred to *orolestes*.

J. A. Allen (1895: 331) described a new species, *Neotoma cinnamomea,* based on 31 specimens from Kinney Ranch, Bitter Creek, Sweetwater County, Wyoming, including therein also two specimens from the Uncompahgre Indian Reservation, Utah, and three from the Little Snake River, Colorado. As diagnostic characters he gave only size and color. Neither the description nor measurements suffice to distinguish *cinnamomea* from *N. c. arizonae.* Indeed, Allen (1896: 249) referred three specimens from Chaco Canyon, New Mexico, to *N. cinnamomea.* This locality is 130 miles east of the type locality of *arizonae* and was included within the range of *arizonae* by Merriam (1893: 111) and Goldman (1910: 96). In his revision of the genus, *Neotoma,* Goldman (1910: 104) synonymized *Neotoma cinnamomea* Allen with *Neotoma cinerea orolestes.* He remarked (p. 105) that "specimens from the type locality of *N. cinnamomea* are paler than typical *orolestes* and grade toward *rupicola.*" Warren (1942: 221), however, revived the name, *cinnamomea,* as a subspecies of *cinerea;* and Hooper (1944: 415) recognized the same name combination for eight specimens from southwestern Wyoming, giving for the first time characters of the skull as well as the skin. Kelson (1952: 239) agreed with Hooper and Warren that specimens from southwestern Wyoming and northwestern Colorado are sufficiently different from *N. c. cinerea, orolestes, alticola,* and *acraia* to warrant recognition as *N. c. cinnamomea;* but he made no comparison with *arizonae,* which he did not consider to be one of the surrounding subspecies. None of the characters given by Warren or Hooper serves to distinguish *cinnamomea* from *arizonae.*

In studying the larger numbers of bushy-tailed wood rats available to me from all parts of western Colorado, I have been unable to find characters to separate specimens from northwestern Colorado from *N. c. arizonae.* In order to decide on the taxonomic status of these specimens, I examined many additional specimens, including pertinent holotypes, from Wyoming, Utah, and Arizona.

The color of the holotype of *arizonae* is the same as that of the only topotype of *cinnamomea* (BSC 88297 ♂) taken in the same month (May) at Kinney Ranch. All 30 other topotypes of *cinnamomea* in the original series were collected from 6 July to 7 August 1895, as was the holotype. Of these, only nine are fully adult (in their second calendar year or older). The females are in much worn pelage, and are paler than the holotype of *arizonae,* as would be expected from the greater wear. The males are molting irregularly. Where the old pelage remains, mainly on the neck and upper back, it is pale as in the females. The new fur, mainly on the lower back and rump, is brighter and more heavily overlaid with black. The first year adults and subadults from Kinney Ranch are in subadult pelage, some with remnants of grayish juvenal pelage on the neck and shoulders. They are on the average lighter, more yellowish buff, than the adults in their second year, but do not differ in color from two specimens of *arizonae* likewise in subadult pelage (MVZ 56691 ♂ and MVZ 56692 ♀) taken in August at Keam Canyon and Oraibi, Arizona. A second year adult (MVZ 89182 ♂) taken at Kinney Ranch on 14 September 1939 is completing molt over all the upper parts. It is rich orange buff on the sides and as heavily overlaid with black on the back as any *arizonae* from northern Arizona or Montezuma County, Colorado. The skulls of the adults from Kinney Ranch differ from the skulls of five *arizonae* from northeastern Arizona (2 second year adults and 1 first year adult from Keam Canyon, 1 second year adult from Walpi, 13 miles west of Keam Canyon, and 1 subadult from Oraibi, 24 miles west of Keam Canyon) as follows: longer dorsal extensions of premaxillaries, slightly longer average diastema, slightly longer average length of maxillary tooth row, and usually wider upper molars in old adults. However, the series of *arizonae* from Montezuma County, Colorado, shows a range of variation in these features which is wide enough to include most of the specimens from Kinney Ranch. Moreover, the characters of the series from Kinney Ranch which represent average differences from the Arizona or Montezuma County series of *arizonae* are not peculiar to *cinnamomea* but are resemblances to *N. c. acraia, N. c. orolestes,* or *N. c. rupicola.*

Specimens from six miles south of Point of Rocks, Wyoming, taken 7 August 1942, have a heavier overlay of black than most topotypes of *cinnamomea,* and the two fully mature adults have upper incisors as wide as the widest incisors of the topotypes. In other features, specimens from the two localities are to me indistinguishable. Likewise, 11 specimens from Antelope Ranch resemble topotypes of *cinnamomea.* Nine of the 11 from Antelope Ranch are in light, grayish-buff subadult pelage. They are uniformly less brightly colored than the two adults.

Three of four specimens from the west side of the Green River, one mile north of the Utah border, in Wyoming, collected in September 1946, are more heavily overlaid with black than specimens of similar age from Kinney Ranch. The skulls are indistinguishable. The skins and skulls (2 adults and 2 subadults) from the west side of the Green River can be matched by comparable specimens from Montezuma County, Colo. Three of the four skulls differ from comparable skulls from northern Arizona in the dorsal branches of the premaxillaries extending farther posterior to the nasals. One of the four (KU 17238 ♂) has a longer diastema. I detect no other differences of geographic significance, in comparison with Arizona specimens. Three first year adults and one immature from one mile north of Linwood, Utah, *in* Sweetwater County, Wyoming, have narrower sphenopalatine vacuities than specimens from Kinney Ranch, suggesting intergradation with *N. c. acraia.* However, in other features they resemble specimens from Kinney Ranch and from northern Arizona. The dorsal branches of the premaxillaries are highly variable in length, extending 0.7, 1.2, 2.0, and 2.5 mm posterior to the nasals. The only skin saved has a long tail and is in worn subadult pelage, molting on the lower sides and thighs. It is more orange buff than specimens of similar age from Kinney Ranch, but lightly overlaid with dusky to about the same degree.

Consideration of the above facts leads to the view that the slight diffierences between populations of bushy-tailed wood rats from southwestern Wyoming and from northeastern Arizona are not sufficiently constant to warrant recognition of more than one subspecies. Since the name, *Neotoma arizonae* Merriam, has priority over the name, *Neotoma cinnamomea* Allen, I here refer specimens from southwestern Wyoming and northwestern Colorado to *Neotoma cinerea arizonae* (see *specimens examined,* p. 270). Although these specimens are not completely typical, their variable differences indicate intergradation with other subspecies rather than evolution of a distinctive form in this region.

Kelson (1949: 417) described a new subspecies, *Neotoma cinerea macrodon,* from the northern edge of the East Tavaputs Plateau, Utah. Since the plateau is physiographically an extension westward of the Roan Plateau in western Garfield and Rio Blanco counties, Colorado, it seemed likely that specimens from that part of Colorado might be referable to *macrodon.* Five adults from western Garfield County are variable in color, two being much darker than the colors specified by Kelson for *macrodon.* Four of the five have longer tails. The skulls agree with the description and measurements given for *macrodon.* In none of these characters, however, do the specimens from western Garfield County exceed the limits of variation seen in the series of *arizonae* from Montezuma County. It seems best to refer all five specimens to *N. c. arizonae.*

According to Kelson (*loc. cit.*), *N. c. macrodon* can be distinguished from *N. c. arizonae* by "Color: Markedly lighter, being buffy rather than tawny, tail duskier above and bushier. Skull: Similar, except the length of the upper molar series is 16 per cent longer in comparable male specimens, sphenopalatine vacuities larger." The specimens from southwestern Colorado examined in the present study include buffy as well as tawny individuals. In general, only the fully mature and old individuals in relatively unworn pelage are tawny or deeply colored. The subadults and young adults, as well as some older adults in worn pelage, are buffy and paler. The range of variation in the length of the maxillary tooth-row in adults of the same series equals 12 per cent of the mean in males and 15 per cent in females. In one female the maxillary tooth-row is as long (10.1 mm) as is given for either sex of *macrodon.* The other characters given above are also noticeably variable in *arizonae* from western Colorado and from Arizona. Since I have not examined any specimens from Utah referred by Kelson to *macrodon,* I do not know whether they can be separated from *arizonae* from southwestern Colorado by any of the characters given. But to me, it seems probable that they will be found to fall within the limits of variability of *arizonae* in nearly all respects.

Durrant (1952: 345, 350) assigned to *N. c. orolestes* a range in Utah which includes the Uinta Basin north of the Colorado and White rivers. Three of the four specimens from the Uinta Basin examined by him "show no intergradation with *N. c. macrodon,* and are referable to *N. c. orolestes*" (*op. cit.*, p. 351). I have examined ten bushy-tailed wood rats from the Uinta Basin. Eight of these are, to me, indistinguishable from the series of *N. c. arizonae* from Montezuma County. One of two adults from the Uncompahgre Indian Reservation (AM 9161, skull only) differs in having wider upper incisors and wider, spatulate anterior ends of nasals, as in *orolestes.* An adult male (BSC 276455) from Vernal has less inflated bullae, as in *orolestes.* The only specimens I have seen from Utah that appear to me to be referable to *orolestes* are from the Uinta Mountains, Daggett County.

The holotype of *N. c. arizonae* has a faint white spot on the nape, which is absent on the single topotype examined. A small white spot on the nape is present in eight specimens of both sexes and all ages from localities as follows: 1 mile south and 22 miles west of

Cortez; 4 miles west and 2 miles south of Cahone; 10 miles west and 5 miles north of Rangely; 11 miles west and 11 miles north of Rangely; Little Snake River; Antelope Ranch, Wyoming; Kinney Ranch, Wyoming; 6 miles south of Point of Rocks, Wyoming. The spots are white to the base of the hairs and vary in size from 12 by 5 millimeters to a mere wisp of pure white hairs. Such spots occur also in a few *N. c. orolestes* (see p. 259 above).

Specimens examined.—Total 130, from Colorado except as specified, as follows: (*1*) Castle Park, 5200 ft., Dinosaur Natl. Mon., 1 (UCM); (*1*) Rimrock above Castle Park, 5600 ft., Dinosaur Natl. Mon., 2 (UCM); (*1*) Mantle's Cave, Dinosaur Natl. Mon., 2 (UCM); (*2*) Snake River, S Sunny Peak, 4 (BSC); (*3*) Little Snake River [7000 ft., Cherokee Crossing, 25 mi. down river from Baggs post office (Allen, 1896: 243)], 4 (AMNH); (*4*) 5 mi. W Craig, 1 (CM); (*5*) Douglas Spring, 6700 ft. [40° 35′ N, 108° 43′ W], 5 (ERW); (*5*) Two Bar Spring [20 mi. NW junction Snake and Bear rivers (F. W. Miller, 1930: 83)], 2 (DMNH); (*5*) Smelter Ranch, 2 mi. SE Greystone, 2 (CM); (*6*) Lily, 1 (BSC); (*7*) Lay, 3 (BSC); (*8*) 8 mi. NE Craig, 1 (CM); (*9*) 11 mi. W and 11 mi. N Rangely, 6000 ft., *in* Moffat Co., 1; (*10*) White River (20 mi. E Rangely), Rio Blanco Co., 1 (BSC); (*11*) 1 mi. S Cross Mountain, 1; (*11*) 5 mi. NW Cross Mountain, 2 (CM); (*11*) S bank Yampa R., 4 mi. NNW Cross Mountain, 2 (CM); (*12*) 6 mi. NE Meeker, 6 (CM); (*13*) 10 mi. W and 5 mi. N Rangely, 5800 ft., 1; (*14*) Douglas Creek, 19 mi. S Rangely, 1 (CM); (*15*) Meeker, 1 (BSC); (*15*) 4 mi. W Meeker, N side White R., 2 (CM); (*16*) 5 mi. W Rangely, 1 (BSC); (*17*) Grand Hogback, 5 mi. S Meeker, 6 (CM); (*18*) Dry Fork, Ute Creek, 6200 to 6500 ft., Rio Blanco Co., 12 (AMNH); (*19*) W Fork Douglas Cr., 8000 ft., 35 mi. S Rangely, *in* Garfield Co., 1 (CM); (*20*) 3 mi. NE De Beque, Mesa—Garfield Co. line, 1 (pick-up, not saved); (*21*) 8 mi. W Rifle, 3 (2 MVZ, 1 BSC); (*22*) 12 mi. SE Rifle, 1 (CNHM); (*23*) Atchee, 6600 ft., 2 (ERW); (*23*) 20 mi. N Mack, 4 (CM); (*24*) State Line, 1 (CM); (*25*) 1 mi. SW Fruita, 3 (DMNH); (*25*) 2½ mi. S Fruita, 4600 ft., S side Colorado R., 1; (*26*) 25 mi. N Grand Junction, Mesa Co., 1 (CM); (*27*) 3 mi. E and 4 mi. S Collbran, 6800 ft., 2; (*28*) Grand Junction, 4600 ft. [S side Colorado R.], 9 (6 ERW, 2 AMNH, 1 MVZ); (*29*) Bedrock, 5150 ft., 2 (ERW); (*30*) about 1 mi. W Cameo, 1 (UCM); (*31*) Coventry, 6800 ft., Montrose Co., 2 (1 ERW, 1 BSC); (*32*) Canyon, 8 mi. NE Dove Creek, 7000 ft., 1 (MVZ); (*33*) 3 mi. W and 2 mi. S Cahone, 7000 ft., Dolores Co., 1; (*33*) 4 mi. W and 2 mi. S Cahone, 7000 ft., Dolores Co., 7; (*34*) 1½ mi. W Dolores, 7000 ft., 1; (*35*) Ashbaugh's Ranch, sec. 31, T. 36 N, R. 18 W, 5350 ft., 4 (2 ERW, 2 BSC); (*36*) Cortez, 6250 ft., rocks S of town, 3 (ERW); (*36*) 5 mi. E Cortez, 2 (CM); (*37*) "Four Corners" [of Utah, Colorado, Arizona, and New Mexico], 5 (DMNH); (*38*) Ute Peak, 1 (DMNH); (*39*) 1 mi. S and 22 mi. W Cortez, 5000 ft., 1; (*39*) 2 mi. S and 24 mi. W Cortez 5000 and 4850 ft., 2; (*40*) 18 mi. N and 1 mi. E Farmington, 6000 ft., San Juan Co., New Mexico, 1; (*41*) Mesa Verde, Spruce Tree House, 1 (DMNH); (*42*) Head of Prater [Canyon, near Pt. Lookout], Mesa Verde Natl. Park, 1 (MVNP).

Neotoma cinerea rupicola Allen

Neotoma rupicola Allen, Bull. Amer. Mus. Nat. Hist., 6: 323, 7 November 1894.

Neotoma cinerea rupicola, Goldman, N. Amer. Fauna, 31: 107, 19 October 1910; Cary, N. Amer. Fauna, 33: 114, 17 August 1911; Hooper, Univ. California Publ. Zool., 42: 422, 17 May 1940; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 220, 1942.

Type.—AMNH No. 8390/6717, adult male, skin and skull; from Corral

Draw, Pine Ridge Indian Reservation (southeastern base of Black Hills), South Dakota; collected 21 August 1894 by W. W. Granger.

Range.—Outside of Colorado the subspecies extends through the Badlands country of southwestern South Dakota, western Nebraska, and southeastern Wyoming. In Colorado its occurrence is limited to the bluffs and buttes of northern Weld and Logan counties. (See map, Fig. 2.)

Diagnosis.—Upper parts pale yellowish tan to creamy buff, lightly overlaid with blackish; tips of ears sparsely covered with pale buff hairs; under parts pure white; tail light gray above with white fringe, pure white below. Skull: robust and angular; rostrum large; interpterygoid fossa wide for the species; sphenopalatine vacuities long and narrow; bullae inflated; upper incisors large.

Description.—An adult in worn pelage taken in July at Battle Cañon, Colorado: size medium for the species; tail about 76 per cent as long as head and body; hind foot of medium length. Pelage: moderately long and dense; tail slightly bushy and distichous, maximum length of lateral hairs 26 mm; longest vibrissae 101 mm. Color: upper parts light orange-buff (M and P: Dorado, 11 C 6; R: Light Ochraceous Buff), moderately overlaid with black; sides brighter (M and P: Peach Blow, 10 B 5; R: near Capucine Buff); ears brownish gray, borders sparsely covered with light hairs (M and P: near Ivory, 10 C 2; R: Light Buff); underparts pure white with band 11 mm wide on sides having hairs gray basally and white distally; tail bicolor, light gray above with white fringe and tip, pure white below; no buffy band under base of tail; feet white.

Skull: robust and angular; rostrum large; zygomatic arches squarish; nasals usually slightly spatulate anteriorly, tapering evenly posteriorly to raggedly pointed ends; premaxillary extensions posterior to nasals moderate; frontonasal region moderately arched and channeled; temporal ridges nearly straight, not widely separated, angular rather than smoothly flaring posteriorly; interparietal between temporal ridges slightly wider than long; incisive foramina long, parallel-sided, slightly pointed anteriorly; anterior palatal spine tapered to thin narrow blade touching vomer; septum deeply notched between palatal spine and vomer; posterior edge of palate convex or square; interpterygoid fossa wide for the species, bounded laterally by curving angular ridges on palatines; sphenopalatine vacuities long and narrow; auditory bullae inflated; incisors large; molars large; anterointernal fold of M1 extending half way across enamel loop.

A juvenile taken in June, 21 mi. N and 5 mi. E Stoneham, Colorado: total length 161 mm; tail 58 mm; eyes closed; immature pelage not yet full grown, hairs extremely short, straight; color same as in adult, except that black-tipped guard hairs on back are so short and closely spaced as to give middorsal region a dark gray general appearance through which the buffy overhairs are slightly visible; ears heavily furred, dark gray on upper outer surface, whitish over entire inner surface; tail covered with extremely short fine hairs, slightly bicolored.

Two subadults from Battle Cañon, Colorado, taken in July: total length 343 and 320 mm; tail 148 and 132 mm; molting from juvenal to subadult pelage; old juvenal pelage on back pale gray (M and P: Kasha Beige, 14 A 2; R: near Light Grayish Olive); new pelage on sides lighter and less vivid (M and P: Vanilla, 10 C 3; R: near Light Buff) than on the single adult; tail well-haired but not bushy, basal hairs fuzzy, tip strongly tufted with long white hairs, tail overwise light gray above.

Comparison.—*N. c. rupicola* differs from *N. c. orolestes* as follows: color of upper parts much lighter, more buffy; fur on belly white to base; tail usually less bushy; incisors larger; rostrum heavier; sphenopalatine vacuities narrower; interpterygoid fossa wider; bullae more inflated.

N. c. rupicola differs from *N. c. cinerea*, *N. c. alticola*, and *N. c. acraia* chiefly in wider sphenopalatine vacuities and lighter color. For comparisons with *N. c. arizonae* see account of that subspecies.

Remarks.—The type and topotypes of *Neotoma cinerea rupicola* from South Dakota are more pallid than specimens from Colorado, being most nearly approached by specimens from Battle Cañon, Colorado. The two subadults from Battle Cañon are scarcely darker than subadult topotypes, and the new pelage on the sides is indistinguishable from that of an adult topotype.

In color, four adults from Pawnee Buttes taken in June and 10 adults from Geary's Reservoir taken in May, June, and November are nearly uniform, and match *N. c. arizonae* from Montezuma County. Those taken in May and June are in worn pelage with fur shorter than in November-taken specimens in fresh pelage, and fur thinner on rump and hind quarters. All are somewhat darker than the adult from Battle Cañon taken in July, more heavily overlaid with blackish, and with a narrower extent of ventral fur pure white to base of hairs. The extent of pure white fur on the belly is at least 50 mm wide in topotypes and in the specimens from Battle Cañon; it is 27 to 42 mm wide in the specimens from Pawnee Buttes, and is only 0 to 35 mm wide in the specimens from Geary's Reservoir. The narrower extent of pure white belly, and the darker upper parts, of specimens from Geary's Reservoir, the westernmost record for the subspecies in Colorado, may be due to some intergradation with *N. c. orolestes.* Although the ranges of these two subspecies are not known to meet in Colorado, they may do so. They almost certainly do meet in Wyoming.

A subadult female (KU 15729) from six miles west of Meriden, Wyoming, has a rudimentary accessory third upper molar on the lingual side of the normal molar and emerging from the same alveolus.

No specimens have been obtained from the two easternmost localities of occurrence (listed as localities *1* and 2 on p. 273 and in Fig. 2). Dr. Edwin C. Galbreath saw a bushy-tailed wood rat at its den at locality *2* in 1949. He saw only a den containing rat pellets and food litter at locality *1*. It is highly probable that *N. c. rupicola* occupies all the bluffs and buttes along the rim of the High Plains north of the South Platte River. No other kind of wood rat is known to occur in the same area.

Specimens examined.—Total 23, from Colorado as follows: (*3*) sec. 3, T. 11 N, R. 54 W, 1 (pick-up, not saved); (*5*) 21 mi. N and 5 mi. E Stoneham, 4700 ft., 4; (*6*) Battle Cañon [sec. 22, T. 11 N, R. 56 W], 3 (DMNH); (*7*) Pawnee Buttes, 4 (ERW); (*8*) 1 mi. N Geary's Reservoir, 10 (DMNH); (*8*) 2 mi. N Geary's Reservoir, 1 (DMNH).

Additional records.—(*1*) E side sec. 22, T. 11 N, R. 52 W (see above, p. 272); (*2*) E side sec. 21, T. 11 N, R. 53 W. (See above, p. 272); (*4*) "Chimney Cliffs (30 mi. NW Sterling)" . . . "valley a mile or so south of the cliffs" (Cary, 1911: 114); (*6*) Avalo (Goldman, 1910: 107).

Neotoma mexicana Baird

Mexican wood rat

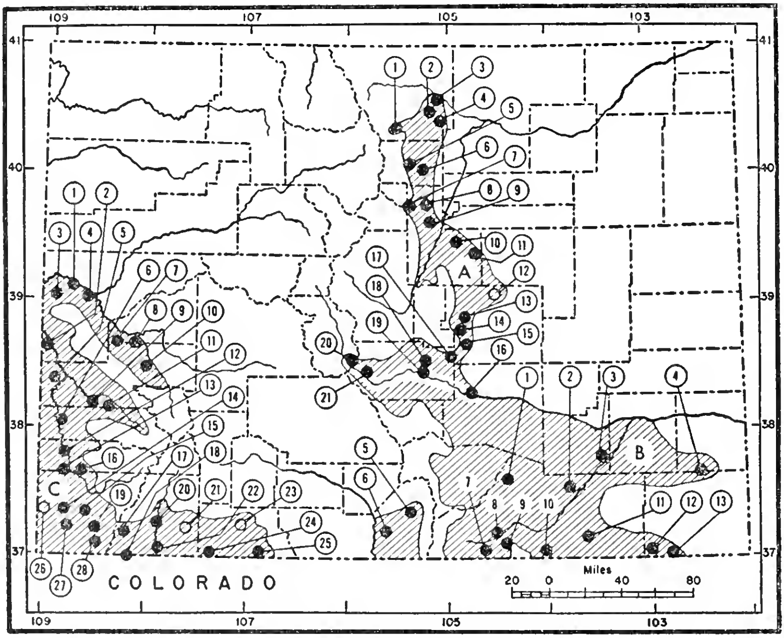
Neotoma mexicana Baird, Proc. Acad. Nat. Sci. Philadelphia, 7: 333, April 1855.

Distribution.—Mountains and plateaus of the Southern Rocky Mountain Region and northwestern Mexico, from northern Colorado south to western Zacatecas and from extreme southeastern Colorado west to the Grand Canyon in Arizona. In Colorado the species occurs at low elevations in southwestern Colorado south of the Colorado and Gunnison rivers, in the San Luis Valley, in the eastern foothills of the Rockies, and east almost to the Kansas state line south of the Arkansas River.

Diagnosis.—Underparts with fur basally gray and distally white or buffy; narrow dusky line around mouth; skull light and smooth; rostrum slender; interorbital region narrow; maxillovomerine notch present; posterior margin of bony palate convex or pointed; interpterygoid fossa narrowly rounded; sphenopalatine vacuities large; upper incisors small; anterointernal enamel fold of M1 deep, cutting more than half way across enamel loop.

Comparisons.—*Neotoma mexicana* can be distinguished from all other species of wood rats in Colorado by the presence of a dark ring or line around the mouth and the absence of pure white fur on the breast (all fur gray basally). The skulls are less easily recognized but differ from those of all other species except *cinerea* and some specimens of *albigula warreni* in having a deep anterointernal fold in the first upper molar. The skulls differ from those of *cinerea* in the smaller rostrum and more curved lateral margins of the interpterygoid fossa. They differ from those of *lepida* in more curved lateral margins of the interpterygoid fossa, larger size, and less inflated bullae. The skulls of *mexicana* differ from those of *albigula, micropus,* and *floridana* in smaller upper incisors and more squarish zygomatic arches (less converging anteriorly).

Skulls of *mexicana* differ also from those of *micropus* and *floridana* in being less strongly arched in the interorbital region and having a maxillovomerine notch in the septum.



NEOTOMA MEXICANA

FIG. 3. Distribution of *Neotoma mexicana.* Ranges of subspecies: A, *N. m. fallax*; B, *N. m. scopulorum*; C, *N. m. inopinata.* Symbols: solid circles, specimens examined; hollow circles, additional records. Numbers refer to localities listed under subspecies accounts (see pp. 278, 283, and 288).

Neotoma mexicana fallax Merriam

Neotoma fallax Merriam, Proc. Biol. Soc. Washington 9:123, 2 July 1894; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 113, 1910, part; Cary, N. Amer. Fauna, 33: 117, 17 August 1911, part.

Neotoma mexicana fallax, Goldman, N. Amer. Fauna, 31:56, 19 October 1910, part; Warren, The mammals of Colorado, Univ. of Oklahoma Press, Norman, p. 213, 1942, part.

Type.—USNM no. 186484, adult male, skin and skull; from Gold Hill ["Denis Gale place, 7500 ft.", "about four miles below Gold Hill toward Boulder" (field notes of Bailey, 1903, and Preble, 1895, respectively)], Boulder County, Colorado; collected 1 November 1889 by Denis Gale.

Range.—In Colorado this subspecies occurs in the eastern foothills of the Rocky Mountains, north to Fort Collins, east on the Arkansas-Platte Divide to Peyton, south to the Arkansas River, and up the Arkansas Valley to Salida. (See map, Fig. 3.)

Diagnosis.—Upper parts grayish brown; frontal wide posteriorly (supraorbital ridges strongly diverging); nasals narrow anteriorly; nasals and dorsal branches of premaxillaries reaching posterior to anterior plane of orbits; skull evenly arched; interparietal long, angular or convex posteriorly; upper incisors of medium size for the species, yellow; molars small.

Description.—Adults in annual molt taken in October at the type locality: size medium; tail about 85 per cent as long as head and body; hind feet medium. Pelage: moderately long; old pelage covering most of upper parts; molt concealed on sides and rump and irregular on back; tail covered with short hairs; longest vibrissae 70 mm. Color: old and new pelages not appreciably different; sides Honeysweet, 11 J 6 (R: Chamois), overlaid with black, the general effect being grayish buff (M and P: near Bamboo, 13 I 6; R: near Grayish Olive, XLVI 19″″); back darker, heavily overlaid with black; ears dark brownish gray; dark eye ring present, sometimes indistinct; underparts whitish, fur basally gray; narrow dusky ring or line around mouth; tail bicolor, black above, white or light gray below; feet white to ankles.

Skull: size medium for the species, evenly arched; rostrum narrow; zygomatic arches nearly parallel-sided in dorsal view; braincase rounded, weakly ridged; nasals narrow anteriorly, lateral margins slightly converging posteriorly, abruptly narrowed near posterior ends which reach a point posterior to anterior plane of orbits; dorsal branches of premaxillae extending 0.0 to 1.9 mm posterior to nasals; interorbital region slightly arched and channeled, narrowly constricted anteriorly; supraorbital ridges strongly diverging posteriorly (frontal 9.3 to 10.5 mm wide at posterior ends of supraorbital ridges); temporal ridges widely flaring on parietals; interparietal variable, usually long and wide, posterior margin convex or angular; incisive foramina tapered toward both ends, anterior ends usually narrower than posterior; anterior palatal spine with right and left sides incompletely fused; nasal septum separated from anterior palatal spine by maxillovomerine notch of variable width; posterior margin of palate convex or bearing a single (sometimes double) point; interpterygoid fossa moderately wide, lateral margins concave; sphenopalatine vacuities long and wide; auditory bullae small to medium, narrow, basioccipital with low median ridge or crest; upper incisors small, yellow; molars small, M1 and M2 subequal; maxillary tooth rows short, nearly parallel; anterointernal fold of M1 deep, cutting more than half way across first enamel loop; small anteroexternal fold of m3 present in approximately half of specimens.

Adults in worn pelage taken in July and August at the type locality: pelage thin and rough, sometimes patches on rump worn so short that only gray basal coloration remains visible; upper parts usually more pinkish than in fresh pelage, less heavily overlaid with black.

Subadults and young adults in subadult pelage taken in July and August at the type locality: Subadult pelage of moderate length, somewhat duller than fresh adult pelage; back less heavily overlaid with black; sides less yellowish; new first autumn pelage usually coming in on sides but still concealed under subadult pelage.

Young subadult (KU 26762) in juvenal pelage, taken in July 3½ mi. W Loveland: total length 245 mm, length of tail 114 mm, length of hind foot 31 mm, weight 79 g; juvenal pelage short and thin, especially on lower back; tail thinly covered with hairs shorter than in adults; postjuvenal molt just beginning on belly, lower sides, and rump; upper parts everywhere gray (M and P: Steel, 47 A 4; R: Deep Mouse Gray) lightly suffused with buff; ears dark gray, edged with white.

Comparisons.—*N. m. fallax* averages slightly grayer and darker than comparable specimens of *N. m. scopulorum* and *N. m. inopinata*, with a heavier overlay of black on the back, but this difference is not so great as the seasonal and age variation in any one of the three subspecies. Individual variation is also marked. Hence color is not a reliable means of recognizing subspecies of the Mexican wood rat. From *scopulorum* to the south, the skull of *fallax* differs in: frontals wider posteriorly, skull smaller and less arched at the base of the rostrum, interparietal longer and less rectangular, upper incisors narrower, molars larger, and nasals narrower anteriorly.

From *N. m. mexicana*, *fallax* differs in: larger skull, frontal wider posteriorly, and nasals projecting posterior to anterior plane of orbits. From *inopinata*, *fallax* differs in: frontal wider posteriorly, upper incisors paler yellow and slightly wider, zygomatic breadth averaging greater, and basicranial ridges less prominent.

Remarks.—The species *N. mexicana* varies much in color, seemingly because of age, season, and individual difference, and, to a lesser extent, geographic variation. Variation in cranial characters due to age is, of course, conspicuous, as in all kinds of wood rats; but individual variation in cranial characters is less noticeable than geographic variation. Consequently the subspecies can be identified more reliably by the skulls than by the skins. The following comments serve to show the extent of individual variation in pelage, and of individual and geographic variation in cranial characters.

Thirteen adults from Loveland taken in May are, on the average, more buffy and less heavily overlaid with black than adults from Gold Hill taken in the period July to October. None of the skins from Gold Hill or Loveland has a buffy band on the pectoral region. Nearly all of the skulls from Loveland have the nasals wider anteriorly and the upper molars wider. Six of 13 mandibles have an anteroexternal fold of m3 present on one or both sides, in comparison with six out of 11 mandibles from Gold Hill.

Three adults in unworn pelage taken in February at South Table Mountain are more richly colored, more orange buff, than adults in fresh pelage from Gold Hill, two of the three being as richly colored as adults of *inopinata* but more heavily overlaid with black. A second-year adult (KU 29182) from one and one-half miles northwest of Golden is in worn summer pelage and has patches of hairs white to the base on the throat and breast. The upper incisors are pale yellow (M and P: Straw, 10 F 2) like incisors of subadult rats, paler than those of normal adults. The posterior palatal margin is double-pointed, as frequently seen in *inopinata*.

Eight of ten adults from ten miles south of Colorado Springs are fairly uniform in color and similar to skins of *fallax* from Gold Hill in subadult and fresh adult pelages. But the two males in old worn pelage taken on 6 September are more pinkish buff than adults in worn pelage from Gold Hill. One of these has a distinct bicolor pattern separated by a sharp molt line over the shoulders and back. Anterior to the line the new pelage is yellowish gray (M and P: 14 I 5), as in the rest of the series. Posterior to the line the old pelage is dull pinkish buff (M and P: French Beige, 13 A 7). The underparts differ from those of the series from Gold Hill in having patches of pure white hairs in the axillae (no gray basal color). Six of the ten skins have incomplete, light buff pectoral bands. The skulls from ten miles south of Colorado Springs resemble those from Gold Hill in most features but differ in: greater width of nasals anteriorly, slightly more arched skull at base of rostrum, and larger molars. These features and the shape of the frontals are, in most specimens, intermediate between those of *fallax* and *scopulorum* and suggest intergradation between these subspecies. The ten specimens are, on the whole, closer to *fallax*, to which they are referred. Three out of ten mandibles from the same specimens have a small anteroexternal fold present in m3.

Three specimens from the north side of the Arkansas River, about 26 miles below Canon City, are like *fallax* in size, dorsal profile of the skull, and shape of the interorbital constriction; but they approach *scopulorum* in shape of the interparietal, size of the rostrum, and size of the molars. They are intergrades referable to *fallax*.

An adult of the year (DMNH 3272) taken in September, two miles northwest of Canon City, differs from comparable specimens from Gold Hill in: hairs on the upper throat, axillary and pubic regions white to base; nasals flaring anteriorly; supraorbital ridges more prominent, less widely diverging posteriorly; and incisive foramina wider posteriorly and more narrowly pointed anteriorly. A second year adult (ERW 3456) taken in June at Howard is dull colored, as in adults of *fallax* from Gold Hill, but is smaller and has a smaller skull, wider nasals, and shorter, more rectangular interparietal. The shape of the interparietal is as in adults of *scopu-*

lorum from Baca County. One of two adults from Salida (ERW 1789, young adult ♂) taken in January is small and has the frontal narrow posteriorly and the supraorbital ridges straight as in *inopinata*. The other (ERW 1809) has the supraorbital ridges concave with the constriction near the middle of the frontal (less anterior) as in *scopulorum*, but the frontal is wide posteriorly as in *fallax*. One of the two skins has a broken, buff pectoral band. On most cranial and pelage characters these specimens are best referred to *fallax*.

The easternmost occurrence of *N. m. fallax* on the Arkansas-Platte Divide, locality *12* on the map (Fig. 3) is not verified by a specimen. There, on 30 May 1950, two miles west and three miles north of Peyton, 7400 feet, I found five dens, mostly under sandstone blocks among ponderosa pines near the summit of the peak marked 7428 feet on sectional aeronautical chart T-4 (Denver). All the dens looked to be unoccupied, and no traps were set. Much of the old food litter consisted of pine needles and cuttings of chokecherry.

Specimens examined.—Total 120, from Colorado as follows: (*1*) Estes Park, 2 (AMNH); (*2*) Arkins, 2 (BSC); (*4*) Loveland, 16 (BSC); (*4*) 3½ mi. W Loveland, 5030 ft., 1; (*5*) [below] Gold Hill, 7500 to 6000 ft., 19 (15 BSC, 4 USNM); (*5*) Salina, 6600 ft., 4 (BSC); (*5*) 5 mi. S Gold Hill, 2 (BSC); (*5*) 2 mi. E and 1 mi. S Gold Hill, 7100 ft., 1; (*5*) Blanchard Ranch, 5 mi. W Boulder, 5800 ft., 2 (UCM); (*6*) Boulder, 11 (2 BSC, 2 USNM, 5 CNHM, 2 ANSP); (*6*) Boulder Canyon, 1 (UCM); (*6*) "near Boulder" 1 (UCM); (*6*) Bear Canyon, 3 mi. S. Boulder, 1 (UCM); (*unspecified*) Boulder Co., 7000 ft., 1 (DMNH); (*7*) Forks Creek [6 mi. E Idaho Springs], *in* Jefferson Co., 4 (UCM); (*8*) Golden, South Table Mountain, 3 (DMNH); (*8*) 1½ mi. NW Golden, 6200 ft., 1; (*9*) Bear Creek, Morrison, 3 (UCM); (*10*) Daniels Park, 7 mi. N and 4 mi. W Castle Rock, 6400 ft., 5; (*11*) Franktown, 1 (DMNH); (*13*) 3 mi. N Colorado Springs, 6000 ft., 12 (8 ERW, 3 AMNH, 1 MVZ); (*14*) 3 mi. SW Colorado Springs, 5500 ft., 1 (ClMNH); (*14*) 5 mi. SW Colorado Springs, 7000 ft., 1 (ClMNH); (*15*) 10 mi. S Colorado Springs, 6500 ft., 8 (ClMNH); (*15*) Van Andert's Spring, Little Fountain Creek, 6200 ft., [sec. 12, T. 16 S, R. 67 W], 2 (ERW); (*16*) Arkansas River, about 26 mi. below Canon City, "1 mi. below Swallows" (field notes of A. Alexander), 3 (MVZ); (*17*) 18 mi. S and 7 mi. W Colorado Springs, 6200 ft., *in* Fremont Co., 2; (*18*) Garden Park, 6 mi. up Red Canyon [= Oil Creek] N of Canon City, 1 (DMNH); (*19*) Canon City, 5 (BSC); (*19*) 2 mi. NW Canon City, 1 (DMNH); (*20*) Salida, 7300 ft., 2 (ERW); (*21*) Howard, 6714 ft., 1 (ERW).

Additional records.—(*3*) Spring Canyon, 5 mi. SW Fort Collins (Goldman, 1910: 57, and Cary, 1911: 117); (*12*) 2 mi. W and 3 mi. N Peyton, 7400 ft. (see above, this page).

Neotoma mexicana scopulorum Finley

Neotoma mexicana scopulorum Finley, Univ. Kansas Publs., Mus. Nat. Hist., 5: 529, 15 August 1953.

Neotoma fallax, Cary, N. Amer. Fauna, 33: 117, 17 August 1911, part.

Neotoma mexicana fallax, Goldman, N. Amer. Fauna, 31: 56, 19 October 1910, part; Warren, Proc. Biol. Soc. Washington, 26: 35, 8 February 1913; Miller, F. W., Jour. Mamm., 12: 432, 11 November 1931; Warren, The mammals of Colorado, Univ. of Oklahoma Press, Norman, p. 213, 1942, part.

Type.—KU no. 37137, old adult male, skin and skull; from 37° 47′ N, 103° 28′ W, three miles northwest of Higbee, 4300 feet, Otero County, Colorado; trapped 16 May 1950 by R. B. Finley, Jr., field number 500516-1.

Range.—In Colorado this subspecies occurs in the canyons and foothills south of the Arkansas River and east to Two Buttes. It is also at the southern end of the San Luis Valley. Its range in northern New Mexico has not been determined. (See map, Fig. 3.)

Diagnosis.—Upper parts grayish buff or grayish yellow, usually brighter on sides; interorbital constriction near middle of frontal rather than anteriorly; supraorbital ridges of frontal concave laterally; skull large, strongly arched at base of rostrum; rostrum wide; nasals wide anteriorly; upper incisors wide, light yellow; molars large, tooth row long; zygomatic arches wide and heavy; interparietal short, wide, posterior margin straight or shallowly angular.

Description—Adults in dense unworn pelage taken in February at Two Buttes Reservoir: size large for the species; tail about 76 per cent as long as head and body; hind feet medium. Pelage: moderately long, thick; tail covered with short hairs; longest vibrissae 80 mm. Color: sides near Raffia, 11 E 6 (R: Cinnamon-Buff), overlaid with black, the general effect being grayish buff (M and P: 13 G 6; R: between Buffy Brown and Citrine-Drab, XL 19‴); back darker, moderately to heavily overlaid with black; indistinct dark eye ring; under parts whitish, fur basally gray except patch of fur pure white to base sometimes present on upper throat; dark line around mouth; tail bicolor, black above, whitish below; feet white to ankles.

Skull: large for the species, strongly arched at base of rostrum; rostrum heavy; zygomatic arches widely spreading, heavy, squarish; braincase moderately ridged and angular; nasals wide anteriorly, lateral margins nearly parallel or converging evenly posteriorly, tapered abruptly at posterior ends which reach a point posterior to anterior plane of orbits; dorsal branches of premaxillae extending 0.5 to 1.2 mm posterior to nasals; interorbital region moderately channeled, narrowly constricted near middle of frontal (instead of anteriorly); supraorbital ridges concave laterally, diverging more strongly posterior to interorbital constriction (frontal 8.7 to 9.5 mm wide at posterior ends of supraorbital ridges); temporal ridges widely flaring on parietals; occipital ridges prominent; interparietal broadly rectangular between temporal ridges, usually short in median line of skull, posterior margin straight or shallowly angular; incisive foramina tapered toward both ends, anterior ends sometimes narrower than posterior; anterior palatal spine usually forming a blade thickened on ventral edge, right and left sides usually incompletely fused; maxillovomerine notch small; posterior margin of palate usually bearing single or double point, sometimes straight; interpterygoid fossa moderately wide, lateral margins concave; sphenopalatine vacuities large; auditory bullae of medium size; basioccipital with low median ridge or crest; upper incisors wide, yellow or yellow-orange; molars large, M1 wider than M2; maxillary tooth-rows long, nearly parallel; anterointernal fold of M1 deep, cutting more than half way across first enamel loop.

Adult (KU 37140♂) in worn pelage taken in May at Two Buttes peak: no molt in evidence; pelage thinner and rougher than in adults of same tooth wear taken in February in unworn pelage; upper parts duller, less heavily overlaid with black; sides less richly yellowish, slightly more pinkish in hue; under parts with no fur white to base (as usual for the species). The skull of this rat has narrower nasals than other adults from Two Buttes and a longer interparietal with a posterior median angle.

Subadult (DMNH 1888) taken in April at Regnier: completing postjuvenal molt to subadult pelage, which is fairly long and thick everywhere except on neck and upper back, where covered by remaining juvenal pelage; upper parts of subadult pelage duller than in adults, sides less buff, more grayish; juvenal pelage grayer than subadult pelage; subadult pelage indistinguishable from subadult pelage of *N. m. fallax.*

Comparisons.—*N. m. scopulorum* is extremely variable in color but averages lighter and richer in color than *fallax,* and about the same as *inopinata. N. m. scopulorum* can be separated from either by the following cranial characters: skull larger, more strongly arched at base of rostrum; interorbital constriction more posterior; supraorbital ridges concave laterally (in contrast to straight, diverging); interparietal shorter in median line, more widely rectangular; zygomatic arches more widely spreading and heavier; upper incisors wider; and molars larger. *N. m. scopulorum* differs from *inopinata* also in paler upper incisors and less prominent basicranial ridges.

N. m. scopulorum is paler than *N. m. pinetorum.* The skulls of these two subspecies are of about the same size, but they differ in other respects as *scopulorum* differs from *fallax* and *inopinata.* From *N. m. mexicana* (to judge from the description and photograph in Goldman's revision), *scopulorum* differs in: larger skull; longer nasals and dorsal branches of premaxillae; more posterior interorbital constriction (supraorbital ridges more concave laterally); wider upper incisors; and larger molars.

Remarks.—The large size and distinctive cranial characters of *N. m. scopulorum* are fairly constant in the northeastern part of its range, but there is a wide range of variation in color. The only two skins from the type locality differ markedly in color. Both specimens (the type and KU 37138, adult ♂) were collected on 16 May 1950 and are in moderately worn pelage. The upper parts of the holotype are much more yellowish than in KU 37138, and are even lighter buff than adults in unworn pelage from Two Buttes. The under parts of the holotype are more extensively white than in almost any other specimen seen of *Neotoma mexicana.* The basal gray coloration, where it is present along the sides of the venter, forms only a narrow intermediate color band extending not more than one third the length of the hairs. An extensive area of the throat, breast, axillae, median belly, and inguinal region is covered by hairs pure white to the skin. The dark line around the mouth is present, as usual for the species. The upper parts of KU 37138 are like those of the adult in worn pelage from Two Buttes peak, described above; the under parts have only small patches of pure white fur on the throat and inguinal region, being elsewhere gray at the base of the fur, as is usual for the species.

In addition to the skins in unworn and worn pelages already described from Two Buttes, an extremely dark specimen is at hand from Two Buttes peak, taken on 9 May 1950. This specimen (KU 37141) is an adult female in moderately worn pelage. The back is dark brownish gray (Taupe, 16 A 6), the sides lighter (a shade lighter than Beaver, 15 A 6). The entire under parts are washed with reddish buff (Grain, 11 B 5) over the gray basal coloration, with a patch of white only in the genital region. The dark eye ring and dark line around the mouth are heavier than usual. The underside of the tail is light gray. The white hind feet are sharply set off from the dark gray ankles.

Four adults and one subadult from Trinidad are intergrades between *N. m. fallax* and *N. m. scopulorum*, perhaps more nearly resembling the latter. In pelage they are indistinguishable from specimens of *fallax* from Gold Hill, less buff than most individuals of *scopulorum* from Baca County. The skulls of the three fully mature adults are large with a wide zygomatic breadth, large rostrum, and large upper incisors as in *scopulorum;* but the upper molars are small and the bullae are rather small and narrow as in *fallax.* Two of the three adults have nasals wide anteriorly as in *scopulorum*, the third, narrow as in *fallax.* In the degree of arching at the base of the rostrum, the shape of the frontal, the shape of the interparietal, and the size of the upper molars, the specimens from Trinidad are intermediate. I refer them to *scopulorum*, but they might with some justification be referred to *fallax.*

Two first year adults from Fisher Peak and Long Cañon are indistinguishable from topotypes of *fallax* of similar age and also resemble a young adult and a subadult from Trinidad, but all are insufficiently mature to show subspecific characters distinctly. Until adequate series are available from southwestern Las Animas County it seems best to regard all specimens from the three localities as representatives of a single uniform population which is intermediate between *fallax* and *scopulorum* but more like the latter. Unfortunately no other specimens are available from the foothill zone south of the Arkansas River where morphological intergradation and ecological transition between *fallax* and *scopulorum* might reasonably be expected to occur.

None of the 16 skins examined from the region east of the Sangre de Cristo Mountains and referred to *N. m. scopulorum* has a buffy pectoral band, but a few show some buff encroaching from the sides onto the edge of the pectoral region.

On a rocky ridge of the San Luis Hills three miles west of San Acacio, in June 1912, E. R. Warren collected 20 Mexican wood rats which display well-marked dichromatism. He has described the specimens and the locality in some detail (Warren, 1913: 35, and 1942: 214). Most specimens are normally colored but some have an unusual distribution of dark pigments. The latter specimens are somewhat melanistic in that the under parts are washed with dull buff (M and P: 11 E 6) instead of white, the underside of the tail is dark gray instead of white, and the feet are white to the bases of the toes instead of entirely white. I have examined the skins and skulls of 16 specimens of this series, including eight melanistic rats and eight normal rats. Males, females, adults, and subadults are included in the color phase. The normally pigmented skins do not differ appreciably in color from specimens of *N. m. scopulorum* in comparable pelage. Some of the melanistic skins are darker gray on the head and back. Only one skin (ERW 4124, adult ♀) has a white tip 12 mm long on the tail, including white hairs both above and below. This individual variation was not noticed on any other wood rat. The length of the tail is, on the average, shorter in the San Acacio series than in other series of *scopulorum* or *fallax*.

The skulls of the adults from three miles west of San Acacio are in average length intermediate between adults of *fallax* from Gold Hill and *scopulorum* from Two Buttes. They resemble *scopulorum* in: robust zygomatic arches, wide rostrum, wide nasals anteriorly, and large molars. They are intermediate between *scopulorum* and *fallax* but usually closer to *scopulorum* in: arching of the skull at the base of the rostrum, shape of the frontal, and width of the upper incisors. The bullae seem to be more nearly round than in either *scopulorum* or *fallax*, the maxillovomerine notch is usually larger, and the nasals usually extend farther posteriorly, frequently extending beyond the dorsal branches of the premaxillae. The above comparisons show the series from San Acacio to be closer to *N. m. scopulorum* than to *N. m. fallax* but slightly different in a few respects from either. The taxonomic status of specimens from the San Luis Hills can be settled with certainty only by more thorough study of the species in New Mexico.

Although the San Luis Hills are composed of dark brown volcanic rocks, it seems unlikely that the darker pigmented specimens of *scopulorum* owe their survival to any selective advantage of their darker color. The parts most strongly dichromatic are those parts least exposed to view on a live rat, that is to say the venter, underside of tail, and hind feet. But the dorsum, which should be most protectively colored, is scarcely darker than on the normally colored rats, and adequately protective, no doubt, in either color phase.

I attempted to obtain additional specimens of *N. mexicana* from three miles west of San Acacio by setting traps there on 26 May 1950, hoping to find out whether melanistic individuals still occur there. The only wood rats I caught were two *N. cinerea orolestes,* which had not been previously reported from the San Luis Hills. They are normally pigmented, for that subspecies.

Of the 28 skulls examined of *scopulorum* from the area east of the Sangre de Cristo Mountains, eight have an anteroexternal enamel fold on m3 and one (BSC 35222/47487) has an anterointernal fold on m3. Of the other 19 mandibles, a few are too old to show such a fold, some others have a projecting angle suggesting an incipient fold, and the rest have a rounded anterior lobe with no extra fold. Of 16 skulls examined from three miles west of San Acacio, eight have an anteroexternal fold on m3 and eight have none, or only a suggestion of an incipient fold. The anteroexternal fold usually shows up more distinctly in young rats with less worn teeth. It tends to be obliterated with wear in later age.

A second-year adult (ERW 4117 ♂) from three miles west of San Acacio has an unusual variation in the pattern of m3, in addition to a sharp anteroexternal fold on each m3. The main internal fold in each m3 is deeper than normal, with its inner edge bent forward and overlapping the posteroexternal fold anteriorly, thus approaching the S-shaped m3 pattern characteristic of *Hodomys,* but without the elongation of the tooth characteristic of *Hodomys.*

Specimens examined.—Total 50, from Colorado as follows: (*1*) 20 mi. E Walsenburg, "Huerfano Co." [?], 1 (DMNH); (*2*) 9 mi. W junction Purgatoire [= Picketwire, = Purgatory] and Chacuaco [= Chaquaqua] creeks, "Red Rock Canyon," (field notes of A. Alexander), 1 (MVZ); (*3*) 3 mi. NW Higbee, 4300 ft., 4; (*4*) Two Buttes Reservoir, 4200 ft., Baca Co., 5 (3 DMNH); (*4*) Two Buttes peak, 4600 and 4650 ft., Prowers Co., 2; (*5*) 5 mi. SSE Fort Garland, 7900 and 7850 ft., 2 (AMNH); (*6*) 3 mi. W San Acacio, 7800 to 8000 ft., 16 (ERW); (*7*) Long Cañon, near Martinsen, 1 (BSC); (*8*) Trinidad, 5 (BSC); (*9*) Fisher Peak [6 mi. SE Trinidad], "about 8000 ft.", 1 (BSC); (*10*) Trinchera, 6 (5 DMNH, 1 AMNH); (*11*) Mesa de Maya, 1 (MZ); (*12*) Furnish Canyon ["Furnace Canyon" on skin labels; approximately 37° 02′ N, 103° 02′ W], Baca Co., 1 (DMNH); (*13*) Regnier, 4500 ft., 37° 00′ N, 102° 50′ W, Baca Co., 4 (2 DMNH).

Neotoma mexicana inopinata Goldman

Neotoma mexicana inopinata Goldman, Jour. Washington Acad. Sci., 23: 471, 15 October 1933.

Neotoma fallax, Warren, Colorado Coll. Publ., Gen. Ser. no. 19, p. 248, January 1906, part; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 113, 1910, part; Cary, N. Amer. Fauna, 33: 117, 1911, part.

Neotoma mexicana fallax, Goldman, N. Amer. Fauna, 31: 56, 19 October 1910, part; Warren, The mammals of Colorado, Univ. of Oklahoma Press, Norman, p. 213, 1942, part.

Type.—USNM (BSC) no. 158395, adult male, skin and skull; from Chuska Mountains, 8800 feet [San Juan County], New Mexico; collected 3 October 1908 by Clarence Birdseye.

Range.—Outside of Colorado the subspecies occurs in northwestern New Mexico, northeastern Arizona, and southeastern Utah. In Colorado it has been found only south of the Colorado and Gunnison rivers at elevations below 7500 feet. (See map, Fig. 3.)

Diagnosis.—Upper parts grayish buff, usually brighter on sides; frontal narrow posteriorly (supraorbital ridges evenly and moderately diverging); upper incisors narrow, yellow-orange; nasals and dorsal branches of premaxillaries reaching posterior to anterior plane of orbits; zygomatic breadth relatively narrow; interparietal long and wide, convex posteriorly, median basioccipital ridge prominent.

Description.—Adults in unworn winter pelage taken in December, February, and April at Coventry: size medium; tail about 80 per cent as long as head and body; hind feet medium. Pelage: moderately long and dense; tail covered with short hairs; longest vibrissae 75 mm. Color: sides light buff (M and P: 11 H 7; R: Cinnamon-Buff) overlaid with black, the general effect being grayish buff (M and P: near Yellow Beige, 13 G 7; R: near Citrine-Drab, XL 19"); back darker, more heavily overlaid with black; ears dark brownish gray; indistinct dark eye ring; underparts whitish, fur basally gray; some specimens (4 out of 7) with complete or incomplete buffy pectoral band; dark line around mouth; tail bicolor, black above, whitish below; feet white to ankles.

Skull: medium size for the species; evenly arched; rostrum slender; zygomatic breadth narrow, sides of zygomata nearly parallel; braincase somewhat narrow, weakly ridged; nasals slightly widened anteriorly, lateral margins slightly converging posteriorly, abruptly narrowed near posterior ends which reach a point posterior to anterior plane of orbits; dorsal branches of premaxillae extending 0.7 to 1.7 mm posterior to nasals; interorbital region slightly arched and channeled or sometimes flattened, narrowly constricted anteriorly; supraorbital ridges moderately diverging posteriorly (frontal 8.8 to 10.3 mm wide at posterior ends of supraorbital ridges), ridges straight or slightly concave; temporal ridges widely flaring on parietals; interparietal variable, usually long and wide, posterior margin convex or angular; incisive foramina tapered toward both ends, anterior ends usually narrower than posterior; anterior palatal spine thin, right and left sides sometimes completely fused, sometimes with line of fusion visible for at least part of length; nasal septum separated from palatal spine by maxillovomerine notch of variable width; posterior margin of palate usually bearing a double (occasionally single) point; interpterygoid fossa moderately wide, lateral margins concave; sphenopalatine vacuities large, highly variable; auditory bullae small, rounded; basioccipital with prominent sharp median crest; upper incisors slender, yellow-orange; molars small, M1 and M2 subequal; maxillary tooth-rows short, nearly parallel; anterointernal fold of M1 deep, cutting more than half way across first enamel loop.

Adults in worn pelage taken in June, 1 mi. E. Naturita: old pelage thin, rough; upper parts more pinkish (less yellowish) buff than in fresh pelage; under parts less white, more gray basal coloration showing through the shorter white tips of hairs.

Subadult (KU 34792) taken in August, 4 mi. W and 2 mi. S Cahone; subadult pelage short, thin on sides; second molt just beginning on lower sides; upper parts duller, grayer buff than adults in fresh pelage; sides less richly colored; subadult pelage less overlaid with black on back than subadult pelage of *N. m. fallax*.

Immature (KU 34773) from 1 mi. SW Gateway, 19 June 1949: total length 242 mm, length of tail 104 mm, length of hind foot 32 mm, weight 66 g; juvenal pelage long, fluffy; molting heavily on sides, new subadult pelage short, concealed under old pelage on sides; tail thinly covered with very short hairs; upper parts light grayish brown (M and P: Goat, 15 C 5; R: near Drab, XLVI 19″″); back lightly overlaid with black; ears blackish, edged with whitish; tail weakly bicolor, gray above, whitish below. The upper parts in juvenal pelage are lighter and more buffy (less gray) than in the juvenal pelage of *N. m. fallax*.

Juvenile (KU 34802) from Spruce Tree Lodge, Mesa Verde, 2 Sept. 1949: total length 142 mm, length of tail 56 mm, length of hind foot 24 mm, length of ear 14 mm, weight 15 g; immature pelage short, dense, stiff, still growing everywhere except on head; fur on back not much longer than on top of head; hairs on tail very short; upper parts light buffy gray; back heavily overlaid with black, the densely spaced black hair tips giving the effect of a dark gray dorsal band; ears blackish, no white edging; tail faintly bicolor, gray above, whitish below.

Comparisons.—*N. m. inopinata* averages lighter in color than *fallax* and about the same color as *scopulorum.* The separation of the subspecies is based primarily on cranial characters. From *fallax, inopinata* differs in: frontal narrower posteriorly, upper incisors deeper yellow-orange and slightly narrower, zygomatic breadth averaging less, and basicranial ridges more prominent. From *scopulorum, inopinata* differs in: upper incisors narrower and deeper yellow-orange, interparietal longer and wider, zygomatic breadth less, and interorbital constriction more anterior (supraorbital ridges less concave). From *N. m. mexicana,* which occurs in southern New Mexico, *inopinata* differs in larger size and nasals projecting posterior to the anterior plane of the orbits. From *pinetorum,* which occurs to the southwest in New Mexico and Arizona, *inopinata* differs in smaller size and paler color.

Remarks.—*N. m. inopinata* resembles *fallax* more closely than it does *scopulorum*. Topotypes of *inopinata* from the Chuska Mountains, New Mexico, are only weakly distinguishable from *fallax*, but specimens from farther north in western Colorado are more easily recognizable. The series of *inopinata* from Coventry better represents the subspecies than the topotypes, and has been used as the basis for description in this account.

Hall (1955: 332), in his map of the distribution of *Neotoma mexicana*, recognized *N. m. inopinata* but included most localities from western Colorado in the range of *N. m. fallax*. All parts of western Colorado from which Mexican wood rats are known to me should be included in the range of *N. m. inopinata*. Specimens from western Colorado (KU 34792, KU 34773, and KU 34772) and one from New Mexico (KU 34817), all listed by him under marginal records of *N. m. fallax*, have been included under *N. m. inopinata* in this report (see p. 288, *specimens examined*, localities *1*, *2*, *13*, and *18*). The record for Bedrock cited by Hall from Warren (1942) is based on 4 specimens, 3 of which I have examined and found to be *N. albigula brevicauda* (see p. 292).

There is a geographic trend in size from north to south, those in the north tending to be smaller. There is considerable individual variation in size of upper molars and in size and shape of the auditory bullae. KU 34815 from 2 miles west and 1 mile south of Chromo has remarkably large, inflated bullae for this species. This specimen has also a wide, dark orange-buff pectoral band extending completely across the body.

None of the six skins examined from the Chuska Mountains, New Mexico, has a buffy pectoral band. Of 18 skins from Montezuma and La Plata counties, 7 have complete pectoral bands and 5 have incomplete or faint bands. Of 14 skins from Dolores, San Miguel, and Montrose counties, 1 has a complete pectoral band and 7 have faint incomplete bands (not crossing the midventral line). Of 19 skins from Mesa and Delta counties, 7 have complete pectoral bands and 4 have incomplete faint bands. There seems to be no geographic regularity in development of the pectoral band.

Three out of five topotypes have a small anteroexternal enamel fold on the m3 of one or both sides. Of 21 skulls from Montezuma, La Plata, and Archuleta counties, 10 have an anteroexternal fold on m3. Of the 22 skulls from Dolores, San Miguel, and Montrose counties, 7 have the anteroexternal fold. And of the 22 skulls from Mesa and Delta counties, 8 have the anteroexternal fold. A first-year adult (KU 34772) from two and one half miles south of Fruita has the anteroexternal fold of m3 almost as deep as that of m2. There seems to be no geographic trend in the occurrence of this fold in any subspecies of *N. mexicana* in Colorado.

A series of Mexican wood rats, 15 males and 9 females, from four miles north of El Rito, 7000 feet, and nine miles northwest of El Rito, 8500 feet, in New Mexico, are referable to *inopinata* but show some approach to *scopulorum.* Two adults (KU 5758 and 5753) and one immature (KU 5763) have the interparietal divided by a suture continuous with the median parietal suture. This anomaly occurs also in *N. floridana campestris* (see p. 318).

Cary (1911: 115) on his map of the distribution of *N. fallax* shows Grand Junction, on the north side of the Colorado River, and both sides of the Grand Valley within the range occupied by "*fallax*" (*inopinata*). This supposed distribution rests on five specimens collected by E. R. Warren on 27, 28, and 29 September 1905, and labeled "Grand Junction, Colo." In my own field work I trapped at three localities in the Grand Valley north of the Colorado but caught only *N. lepida sanrafaeli.* All records except Warren's for *N. mexicana* in the Grand Valley are from the south side of the Colorado and Gunnison rivers. I therefore looked up Warren's diary for 1905 at Colorado College, Colorado Springs, to ascertain on which side of the river he obtained his specimens. His dairy is detailed and informative, providing a pleasant insight into the activities and personality of Colorado's pioneer mammalogist, as well as glimpses of Colorado in his day. His entries for September, 1905, reveal that he traveled to Grand Junction by train and hiked into the field from there on foot, returning each evening to his hotel in the city. He collected five *N. mexicana* as well as numerous *N. cinerea* and other rodents on 27, 28, and 29 September. His diary entry for 26 September 1905, pp. 75-76, reads (in part) as follows: "I was up in good season, had breakfast, and started out with my knapsack. I went south, crossed the Grand [= Colorado River] on a bridge, then cut across country to another bridge over the Gunnison, and then turned and went up along the Gunnison. . . . There was a ranch here, setting back near the sandstone bluffs which are a few hundred yards back from the river. I set several mouse traps in the brush near the river, and then turned toward the rocks, and there found many signs of *Neotoma.* Put out a number of Rat and Mouse traps. . . ."

Warren's entries on the following days record that he salted the skins of rats collected on 27 September and put them away until the 30th, when he made them up into study skins. Other rodents taken on the 27th were put up that afternoon fresh, using no salt. (Warren's wood rat skins that have been salted are usually recognizable by the granular appearance and feel of the skin.) On later days he hiked north of town over the flat "desert Valley" but found little of interest and decided it would be more profitable to continue trapping and hunting south of the river rather than to the north.

Since, according to Warren's diary, his wood rats labeled "Grand Junction" were trapped south of the Colorado River and west of the Gunnison River, no specimens of *N. mexicana* are known to me from north of the Colorado River. Nor are there any from northeast of the Gunnison River, although Cary (1911: 117) stated, "A very few nests [dens] seen in the bluffs along the North Gunnison River near Hotchkiss appeared to belong to *fallax* rather than to *orolestes*." I searched for dens along both sides of the North Gunnison River up as far as Paonia and found no dens and very little suitable shelter. Farther up I trapped two specimens of *N. cinerea orolestes* from the sandstone cliffs one mile northeast of Bowie, 6300 feet. Perhaps the dens seen by Cary were all of *orolestes*.

Specimens examined.—Total 89, from Colorado except as specified, as follows: (*1*) 2½ mi. S Fruita, 4600 ft., S side Colorado River, 1; (*2*) 1 mi. SW Gateway, 4600 ft., 4; (*2*) 2½ mi. S and 1 mi. W Gateway, 5300 ft., 1; (*3*) Sieber Ranch, Little Dolores Creek, 5675 ft. [6 mi. E Utah line (Warren, 1913: 9)], 5 (ERW); (*4*) Grand Junction, 4600 ft. [S side Colorado River], 4 (3 ERW, 1 MVZ); (*5*) 2 mi. E Paradox, 1 (DMNH); (*6*) 8 mi. N and 3 mi. E Egnar, 5800 ft., 2; (*7*) "17 mi. SW" [?] Delta, Delta Co., 2 (DMNH); (*8*) "8 mi. W [?] Olathe, Delta Co." [8 mi. NW, *in* Delta Co., according to R. J. Niedrach], 4 (DMNH); (*9*) 1 mi. E Naturita, 5900 ft., 6; (*10*) 7½ mi. W Montrose, 6000 ft., 3; (*11*) Coventry, 6800 ft., Montrose Co., 8 (5 ERW, 2 BSC, 1 AMNH); (*11*) near Coventry, 6800 ft., *in* San Miguel Co., 2 (ERW); (*12*) Canyon, 8 mi. NE Dove Creek, 7000 ft., 1 (MVZ); (*13*) 1 mi. N Cahone, 6900 ft., Dolores Co., 3; (*13*) 3 mi. W and 2 mi. S Cahone, 7000 ft., Dolores Co., 1; (*13*) 4 mi. W and 2 mi. S Cahone, 7000 ft., Dolores Co., 3; (*14*) Ashbaugh's Ranch, sec. 31, T. 36 N, R. 18 W, 5350 ft., 6 (5 ERW, 1 AMNH); (*15*) Cortez, 6250 ft., rocks S of town, 1 (ERW); (*15*) 5 mi. E Cortez, 6400 ft., 1; (*16*) 6½ mi. E and 2 mi. S Cahone, 6800 ft., Dolores Co., 1; (*17*) 5 mi. E and 12 mi. S Mancos, 6800 ft., *in* La Plata Co., 1; (*18*) 18 mi. N and 1 mi. E Farmington, 6000 ft., San Juan Co., New Mexico, 4; (*19*) Headquarters area, 6950 ft., Mesa Verde Natl. Park, 3 (1 MVZ); (*19*) Spruce Tree House, Mesa Verde Natl. Park, 2 (MVZ); (*19*) Cliff Palace, Mesa Verde Natl. Park, 1 (MVZ); (*20*) 2 mi. E Durango, 7500 ft., 1; (*20*) 3 mi. W and 1 mi. S Durango, 7200 ft., 1; (*22*) Bondad, 15 mi. S Durango, 6050 ft., 5; (*22*) 2 mi. NE Bondad, 6100 ft., 3; (*24*) Arboles, 2 (BSC); (*25*) 2 mi. W and 1 mi. S Chromo, 7200 ft., 1; (*27*) Ute Peak, "20 mi. S" [?] Cortez, 4 (DMNH); (*28*) 6 mi. E and 17 mi. S Cortez, 5600 ft., 1.

Additional records.—(*21*) Bayfield (Cary, 1911: 117); (*23*) Pagosa Springs (Cary, 1911: 117); (*26*) near McElmo (Cary, 1911: 117).

Neotoma albigula Hartley

White-throated wood rat

Neotoma albigula Hartley, Proc. California Acad., Sci. (Ser. 2), 4: 157, 9 May 1894.

Distribution.—Arid regions of the southwestern United States and northern Mexico, from the Colorado Desert, California, to the eastern edge of the Staked Plains, Texas, and from the Arkansas River, Colorado, south to Hidalgo. In Colorado the species occurs at low elevations in the Dolores and San Juan drainage systems and on the Great Plains south of the Arkansas River.

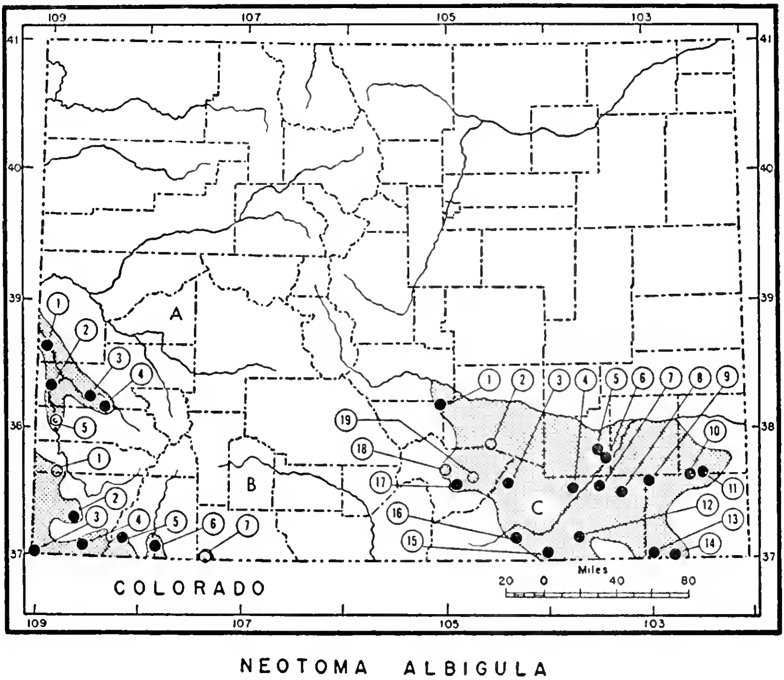


FIG. 4. Distribution of *Neotoma albigula.* Ranges of subspecies: A, *N. a. brevicauda*; B, *N. a. laplataensis*; C, *N. a. warreni.* Symbols: solid circles, specimens examined; hollow circles, additional records. Numbers refer to localities listed under accounts of subspecies (see pp. 293, 297, and 308).

Diagnosis.—Size small to medium; throat, breast, and inguinal region white to base of hairs; pelage short; skull smooth; rostrum stout; supraorbital region less arched than cranium; dorsal margin of foramen magnum deeply concave; interparietal between parietal ridges noticeably wider than long; anterior palatal spine pointed; maxillovomerine notch present; posterior margin of palate concave; sphenopalatine vacuities widely open; upper incisors large; anterointernal fold of M1 shallow or moderate.

Comparisons.—*Neotoma albigula* is a species of such diversity of size, color, and cranial characters as to render difficult any concise characterization of the species which would distinguish all of its races from the other round-tailed wood rats. It can be readily separated from *N. mexicana* by the pure white fur on the breast (absence of gray basal coloration), stouter upper incisors, and shallower anterointernal fold of M1. In addition, the rostrum is heavier, the posterior extensions of premaxillaries usually longer, and the posterior margin of the bony palate usually concave instead of pointed.

N. albigula can be distinguished from *N. lepida* by: size larger; pelage shorter, coarser; breast with larger area of fur pure white to base; upper incisors larger; rostrum heavier; anterior palatal spine slender-pointed, not stout; molars larger. In addition, the two species, in Colorado, are geographically separated by the Colorado River, *albigula* occurring only on the south side and *lepida* only on the north side of the river.

N. albigula differs from *N. floridana* in: size smaller; ears larger; skull less arched; anterior palatal spine pointed (not forked); septum divided by maxillovomerine notch; interpterygoid fossa usually wider; sphenopalatine vacuities wider; bullae rounder. In addition, the two species, in Colorado, are geographically separated by the Arkansas River, *albigula* occurring only on the south side and *floridana* only on the north side of the river.

N. albigula is most easily confused with *N. micropus*, from which it usually differs in browner, less gray pelage. However, at least one subspecies, *N. a. warreni*, cannot always be separated from *N. micropus canescens* by color. *N. albigula* can be distinguished most reliably from *N. micropus* by the presence of a maxillovomerine notch in the septum, and by the baculum having a more slender, constricted shaft and less massive base. Most specimens of *albigula* also differ in the less arched supraorbital region, more concave or notched supraoccipital margin of foramen magnum, and narrower interpterygoid fossa. Specimens in the flesh, when compared with *micropus* of comparable age, were recognized in the field by the usually browner color, more angular parietal ridges (exposed by slitting the skin at the nape), and narrower fore- and hind-feet. The width of the feet is not useful for separating dry study skins of the two species, because of shrinkage.

Neotoma albigula brevicauda Durrant

Neotoma albigula brevicauda Durrant, Jour. Mamm., 15: 65, 15 February 1934.

Type.—MVZ no. 57347, adult male, skin and skull; from Castle Valley, about 15 miles northeast of Moab, Grand County, Utah; collected 13 May 1933 by S. D. Durrant.

Range.—In Colorado this subspecies occurs up the Dolores and San Miguel valleys as far as Gladel and Coventry. Outside of Colorado it has been reported only from the type locality in Utah. (See map, Fig. 4.)

Diagnosis.—Upper parts yellowish to pinkish buff overlaid with black or dusky; skull evenly arched; squamosal root of zygomatic arch forming a nearly right angle; incisive foramina long, wide posteriorly; upper incisors wide; rostrum wide; temporal ridges widely flaring; maxillovomerine notch large; interpterygoid fossa narrow.

Description.—Adults in worn pelage taken in June 1 mi. SW Gateway: size medium; tail 78 per cent as long as head and body (average of four with unbroken tails); hind feet of medium length; ears large. Pelage: thin, long for the species; tail covered with short hairs; longest vibrissae 77 mm. Colors: upper parts Dorado, 11 C 6 (R: Light Ochraceous Buff), overlaid with black, the general effect being New Cocoa, 7 A 10 (R: near Fuscous, XLVI 15''''j); sides richer, less overlaid with black; ears dark brownish gray, faintly edged with whitish, a small light spot below ear; underparts white, fur basally gray except on throat, breast, and inguinal region where white to base; tail bicolor, black above, white below; feet white.

Skull: size medium for the species; rostrum wide; zygomatic arches nearly parallel or slightly converging anteriorly, zygomatic root forming nearly a right angle; braincase arched; nasals wide anteriorly, lateral margin concave or straight, more strongly tapered posteriorly; dorsal branches of premaxillae extending 2.3 to 2.9 mm posterior to nasals; frontonasal region arched equally with braincase or slightly less; supraorbital ridges weak, shallowly concave or straight in dorsal aspect; temporal ridges widely flaring, widest apart on a line near middle of parietals, curving inward posteriorly; interparietal wide between temporal ridges, with median posterior angle rounded; weak occipital crest, but no tubercle present; dorsal margin of foramen magnum concave or notched; incisive foramina long, wide, greatest width on a line one third of length from posterior ends; maxillovomerine notch large, cutting deeply into vomer; anterior palatal spine narrow, tip narrowly in contact with projecting point of vomer; posterior margin of palate bearing a minute point; interpterygoid fossa narrow or of median width, nearly U-shaped, extending forward not quite to anterior border of M3; sphenopalatine vacuities large; bullae moderately narrow; upper incisors wide, enamel deep yellow-orange; molars small; anterointernal fold of M1 shallow, almost absent.

A subadult female (KU 34748) taken 19 June 1949, 1 mi. SW Gateway: total length 263 mm; length of tail 110 mm; weight 80 g; molting to subadult pelage; worn, thin, juvenal pelage on head, neck, and forward half of back; subadult pelage elsewhere long, dense; upper parts grayer than in adults;

sides much duller, ivory to straw-colored, overlaid with gray; ears darker, white edging more marked; old pelage on head and upper back grayer than new pelage; tail gray above, shorter-haired than in adults, annulations barely visible; braincase smoothly rounded, squamosal root of zygomatic arches obliquely angled, as in *N. a. laplataensis;* anterointernal fold of M1 extending nearly half way across first enamel loop.

A juvenal female (KU 34753) taken 21 June 1949, 1 mi. SW Gateway: total length 160 mm; length of tail 60 mm; length of hind foot 26 mm; length of ear 18 mm; weight 24.6 g; not molting; pelage long and dense; upper parts darker gray than subadult and adult; sides grayer, with only faint tinge of straw color; collar-like band of long hairs across shoulders, set off by bands of thinner, worn hairs before and behind; tail extremely short-haired, annulations slightly visible; M1 slightly worn; M2 unworn, ⅔ as high as M1; M3 not yet erupting from alveolus.

Comparisons.—Specimens of *N. a. brevicauda* from Colorado are more brownish that *N. a. warreni* and more richly colored on the sides but cannot be distinguished from *N. a. laplataensis* or *N. a. albigula* by color. They differ cranially from all three in the nearly square squamosal roots of the zygomatic arches, the posteriorly wider incisive foramina, the wider upper incisors, and the heavier rostrum.

Remarks.—In April 1908, E. R. Warren collected three wood rats from Bedrock and two from Coventry in Montrose County. He identified all of them as *Neotoma fallax* (now a subspecies of *N. mexicana*), the only form of the subgenus *Neotoma* then recognized from southwestern Colorado. Examination of Warren's specimens revealed that all three from Bedrock (ERW 2971, ERW 2979, and AMNH 28835) and one from Coventry (AMNH 28834) belong to the species *albigula* and are best referred to *N. a. brevicauda,* which was described in 1934 by Durrant, from Castle Valley, Utah, and has been known since then only from the type locality. Warren's catalog lists an additional specimen (ERW 2973 male) from Bedrock as *N. fallax,* but I was unable to find it. This specimen may also be a *N. albigula brevicauda,* or it may be a *N. mexicana inopinata,* the race of *N. mexicana* at present recognized from southwestern Colorado. There is no reason to doubt that both species occur at Bedrock, for both have been collected at Coventry and at Gateway.

The five adults from one mile southwest of Gateway, used for description of this subspecies as it is found in Colorado (see p. 291) do not agree in all respects with topotypes of *N. a. brevicauda,* known to me only by the original description. The former are not as distinctly differentiated from *N. a. laplataensis* as are topotypes of *brevicauda.* Specimens from southwest of Gateway differ from topotypes in longer tail, longer hind foot, more U-shaped interpterygoid fossa, and in having usually a small point on the posterior margin of the palate, thus resembling *laplataensis* in these characters. Probably the population in Castle Valley, Utah, between the La Sal Mountains and the Colorado River, is more isolated as well as farther north than any other population of *N. albigula* in Colorado or Utah.

An old adult female (ERW 2979) from Bedrock differs from adults from one mile southwest of Gateway in narrower upper incisors (thus approaching *N. a. laplataensis*) and more V-shaped interpterygoid fossa (as in topotypes of *brevicauda*). ERW 2971, adult female, from Bedrock is an intergrade between *brevicauda* and *laplataensis.*

The southernmost locality for this subspecies, plotted (*5*) on the map (see Fig. 4), is not verified by a specimen. The place is Gladel, or "Slick Rock", in Dolores Canyon, 8 miles north and 3 miles east of Egnar, where traps were set for wood rats on two occasions, 17 June and 20 August, 1949. The only rats caught there were two *N. mexicana inopinata.* Analysis of the dens of these rats and a brief survey of other dens revealed that at least two kinds were present, one having a dense midden of cactus spines typical of *N. albigula.* None of the cactus middens was fresh, indicating that the former occupants had disappeared. Indeed, one large midden was stratified, indicating alternate occupation of the same den shelter by *N. albigula* and *N. mexicana.* For detailed descriptions of dens at "Slick Rock" see the ecological account of *N. mexicana,* page 421. This locality (*5*) is in the zone of intergradation between *N. a. brevicauda* and *N. a. laplataensis,* and is included in the range of *brevicauda* on physiographic grounds, for there seems to be only intermittent contact between white-throated wood rats of the Dolores and San Juan drainage systems.

Specimens examined.—Total 13, from Colorado as follows: (*1*) 1 mi. SW Gateway, 4600 ft., 8; (*2*) Bedrock, 5150 ft., 3 (2 ERW, 1 AMNH); (*3*) 1 mi. NE Naturita, 5900 ft., 1; (*4*) Coventry, 6800 ft., Montrose Co., 1 (AMNH).

Additional records.—(*5*) 8 mi. N and 3 mi. E Egnar, 5800 ft. (by auto altimeter) [5500 ft., on U. S. G. S. Topo. Map. Paradox Valley Quadrangle], (see above, this page).

Neotoma albigula laplataensis Miller

Neotoma albigula laplataensis Miller, Proc. Colorado Mus. Nat. Hist., 12: 2, 22 July 1933.

Neotoma albigula albigula, Miller, Jour. Mamm., 12: 432, 11 November 1931.

Neotoma albigula laplatensis [sic], Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 212, 1942.

Type.—DMNH no. 721, adult male, skin and skull; from Bondad [37° 03½′ N, 107° 53′ W], La Plata County, Colorado; collected 20 June 1913 by L. J. Hersey.

Range.—In Colorado this subspecies occurs in the southwestern corner below 7000 feet in the canyons of the San Juan drainage system. Outside of Colorado its limits have not been established, but may be placed roughly at the limits of the San Juan drainage in Utah, Arizona, and New Mexico. (See map, Fig. 4.)

Diagnosis.—Size small; upper parts yellowish to orange buff overlaid with black or dusky; skull small; frontonasal region less arched than braincase; supraorbital ridges weak, shallowly concave or straight in dorsal aspect; bullae narrow; squamosal root of zygomatic arch forming an oblique angle; incisive foramina spindle-shaped, short and narrow; temporal ridges widely flaring on parietals; interparietal large, with prominent median posterior angles; maxillovomerine notch large; interpterygoid fossa narrow.

Description.—An adult female (KU 34764) taken 24 October 1949, 2 mi. NE Bondad: size rather small for the species; tail 78 per cent as long as head and body; hind feet of medium length; ears large. Pelage: fresh and thick, long and soft for the species; tail covered with short hairs; longest vibrissae 66 mm. Color: upper parts Raffia, 11 E 5 (R: Warm Buff), back heavily overlaid with black, general effect being Rubber +, 15 H 8 (R: near Olive Brown, XL 19‴ 1); sides richer, less overlaid with black; ears dark brownish gray, faintly edged with whitish, a small whitish spot below ear; underparts white, fur basally gray except on throat, breast and inguinal region where white to base; tail bicolor, black above, white below; feet white.

Skull: small and light for the species; rostrum small; zygomatic arches narrow, squamosal root forming oblique angle; braincase strongly arched, smooth; nasals narrow anteriorly, nearly straight-sided; dorsal branches of premaxillae extending 2.0 mm posterior to nasals; frontonasal region only slightly arched; supraorbital ridges weak, straight in dorsal aspect; temporal ridges widely flaring, widest apart on a line near middle of parietals, curving strongly inward posteriorly; interparietal wide between temporal ridges, with prominent median posterior angle; slight external occipital tubercle or incipient crest; dorsal margin of foramen magnum deeply concave; diastema short; incisive foramina spindle-shaped, short, narrow; maxillovomerine notch large, cutting deeply into vomer; anterior palatal spine narrow, tip broken (in holotype, tip narrowly in contact with projecting point of vomer); posterior margin of palate bearing minute point; interpterygoid fossa narrow, nearly U-shaped; sphenopalatine vacuities long, moderately wide; bullae small, narrow; upper incisors narrow, enamel yellow-orange; molars small; anterointernal fold of M1 shallow.

A subadult (KU 34766) taken 15 June 1949 at Bondad: total length 268 mm; length of tail 117 mm; weight 106 g; molt to subadult pelage had been nearly completed; worn, thin juvenal pelage on head and neck; elsewhere new subadult pelage moderately long and dense; upper parts grayer than adult from 2 mi. NE Bondad; sides much duller; ivory to straw-colored overlaid with gray; tail gray above, shorter-haired, annulations barely visible through hairs;

cranial sutures loose; interparietal extremely wide, with median posterior angle as in adult; no external occipital tubercle; posterior palatal margin concave, without point.

Comparisons.—*N. albigula laplataensis* is more yellowish or brownish than *N. a. warreni* but cannot be distinguished from *N. a. albigula* or *N. a. brevicauda* by color. *N. a. laplataensis* differs cranially from all three in the flatness of the frontonasal region (between the maxillary roots of the zygomatic arches), which is less arched than the braincase. In the other subspecies the frontonasal region is usually more arched than the braincase or equally arched. From *albigula, laplataensis* differs also in longer fur and smaller bullae. From *brevicauda, laplataensis* differs also in shorter and narrower incisive foramina and the more nearly square squamosal roots of the zygomatic arches. For other differences from *warreni* see the account of that subspecies, page 299.

Remarks.—The type is a second year adult slightly smaller than the adult female (KU 34764) described above from two miles northeast of the type locality and is in worn summer pelage. The back of the type is lighter and more buffy, being more thinly overlaid with dusky (not black). The tail is lighter above with a narrower gray (rather than black) dorsal band. The skull of the type has longer (2.8 mm) dorsal extensions of the premaxillaries posterior to the nasals, wider incisive foramina, more concave lateral margins of the interpterygoid fossa, and the anterointernal fold of M1 cutting nearly half way across the enamel loop. An adult female topotype (KU 34765) taken on 15 June 1949 has worn, smooth pelage. The dorsum is nearly as dark as in KU 34764, the sides slightly more pinkish, and the tail dark gray above. The skull is slightly larger, with wider upper incisors and a smoothly concave posterior palatal margin.

Two young adults of the year (KU 34760 and 34762) collected in August 5 miles east and 15 miles south of Mancos are of nearly the same size as the type and are in thin subadult pelage. Both specimens are less brightly colored than KU 34764 from two miles northeast of Bondad. The skull of KU 34760 has a larger braincase, and both lack the external occipital tubercle.

Three specimens from 6 miles east and 17 miles south of Cortez, Montezuma County, in color resemble specimens of comparable age from La Plata County. The skulls have the nasals wider anteriorly, and the two adults have wider upper incisors. A young adult male (KU 29181) from 2 miles south and 4 miles west of

Cortez, taken on 12 September 1948, was in second molt on the upper sides and rump. Both the first autumn and the subadult pelages are paler than the fresh adult pelage of KU 34764 from two miles northeast of Bondad, and both pelages lack the bright buff hue on the sides. The skull differs in the abruptly widened anterior ends of nasals, absence of an external occipital tubercle, the minutely forked tip of the anterior palatal spine, and the wider more orange upper incisors. Three skulls from Four Corners, like other skulls from Montezuma County, have wider anterior ends of nasals and wider, more orange upper incisors than specimens from La Plata County, thus approaching *N. a. brevicauda,* which occurs to the northwest.

Although a longer and heavier maxillary tooth-row has been attributed to *N. a. laplataensis* in the original description in comparison with topotypes of *N. a. albigula,* I can find no significant differences by comparisons of series of *laplataensis* from La Plata and Montezuma counties, Colorado, and of *albigula* from near the type locality and other localities in Pima and Pinal counties, Arizona, and of *brevicauda* from Mesa County, Colorado. The only geographic variation observed in this character is in southeastern Colorado, where *N. a. warreni* has a longer and heavier tooth-row than any of the series cited above.

The northernmost locality for this subspecies, plotted *1* on the map (see Fig. 4), is not verified by a specimen. The place, one mile north of Cahone, 6900 feet elevation, Dolores County, is also near the upper limit of elevation for *N. albigula* in Colorado and is nearly on the divide between Cross Canyon, a tributary of the San Juan drainage, and Dolores Canyon. There, near the head of a branch of Cross Canyon, I found a den (490819-2) with a large midden of cactus spines typical of *N. albigula.* Traps were set three nights in August, 1949, without success. At the numerous other dens without cactus middens in the area, several *N. mexicana inopinata* and *N. cinerea arizonae* were trapped. For a description of den 490819-2 see the ecological account of *N. albigula,* page 461. Descriptions of other dens in the vicinity of Cahone are given under accounts of those subspecies (see p. 418 and p. 376). This locality (*1*) is between the known ranges of *N. a. laplataensis* and *N. a. brevicauda,* and if specimens can be obtained from here they will probably prove to be intergrades. The divide narrowly separating the Dolores Canyon from the heads of the San Juan tributaries seems to constitute a partial or intermittent barrier between populations of white-throated wood rats in the two drainage systems.

In his account of "*Neotoma fallax*" Cary (1911: 118) states, in part, "in the bluffs along the San Juan River at Arboles these rats often construct their nests [houses] entirely of the spiny branches of tree cactuses. . . ." Two specimens of *N. mexicana inopinata* were taken by Cary at Arboles, but it is not clear whether these rats were caught at the cactus houses mentioned above or at some other kind of den. On 15 November 1949 I found nine dens along the low sandstone cliffs on the west side of the Piedra River at Arboles. All were in rock crevices or under boulders and none contained sizeable quantities of cactus joints or spines. The dens contained masses of cuttings of soft-leaved shrubs, and looked to be typical of *N. mexicana.* Of the many dens of *N. m. inopinata* examined in the present study, none was constructed of cactus. The only houses or dens studied in southwestern Colorado composed of any kind of cactus joints were made by *N. albigula laplataensis* and *N. a. brevicauda.* Under a large boulder two miles south of Arboles, south of the San Juan River, I found a den with a midden containing cactus spines, but not in the large quantity usually associated with *N. albigula.* I could not be certain whether this den had been made by *N. mexicana* or *N. albigula.* I caught no rats at either site near Arboles. The dens constructed of tree cactus at Arboles, and mentioned by Cary, probably were made by *laplataensis,* which is known to occur at Bondad in the Animas Valley, 27 miles west of Arboles. Arboles is indicated on the map, Fig. 4, as 7, representing the easternmost record of occurrence of *laplataensis* in Colorado.

Specimens examined.—Total 15, from Colorado as follows: (2) 2 mi. S and 4 mi. W Cortez, 5900 ft., 1; (3) "Four Corners" [of Utah, Colorado, Arizona, and New Mexico], 3 (DMNH); (4) 6 mi. E and 17 mi. S Cortez, 5600 ft., 3; (5) 5 mi. E and 15 mi. S Mancos, 6500 ft., *in* La Plata Co., 3; (6) Bondad, 15 mi. S Durango, 6050 ft., 3 (1 DMNH); (6) 2 mi. NE Bondad, 6100 ft., 2.

Additional records.—(1) 1 mi. N Cahone, 6900 ft., Dolores Co., (see above, p. 296); (7) Arboles (see above, this page).

Neotoma albigula warreni Merriam

Neotoma albigula warreni Merriam, Proc. Biol. Soc. Washington, 21: 143, 9 June 1908; Goldman, N. Amer. Fauna, 31: 34, 19 October 1910; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 111, 1910; Cary, N. Amer. Fauna, 33: 116, 17 August 1911; Warren, The mammals of Colorado, Univ. of Oklahoma Press, Norman, p. 212, 1942.

Neotoma albigula, Warren, Colorado Coll. Publ., Gen. Ser. no. 19, p. 248, January 1906.

Type.—USNM no. 151051, adult male, skin and skull; from Gaume's Ranch [sec. 21, T. 28 S, R. 50 W], 4600 feet, Baca County, Colorado; collected 28 November 1907 by Merritt Cary.

Range.—In Colorado this subspecies occurs south of the Arkansas River and east of the Rocky Mountains, ranging almost to the Kansas state line. Outside of Colorado it has been found only in Union County, New Mexico, and Cimarron County, Oklahoma. (See map, Fig. 4.)

Diagnosis.—Upper parts light bluish or brownish gray with suffusion of buffy or pinkish becoming more noticeable on sides and cheeks; skull robust and angular for the species; temporal ridges bending sharply inward at posterior edge of parietals; rostrum arched at base; braincase arched; notch in septum between vomer and palatal spine small; interpterygoid fossa variable in shape, usually wide; anterointernal fold of M1 deep for the species, cutting about half way across first enamel loop.

Description.—Adults in worn pelage taken in May, 1 mi. NW Higbee: size medium; tail approximately 72 per cent as long as head and body; feet and ears of medium length for the species. Pelage: moderately short for the genus, though not differing much in length from that of *N. albigula albigula;* tail covered with short hairs; longest vibrissae 78 mm. Color: upper parts bluish gray to light brownish gray with blackish overlay, the general effect being Jack Rabbit (39 A 2) to Log Cabin + (15 A 5) or Sandy-Beige (14 A 3) (R: Neutral Gray to Hair Brown or Light Drab); sides, legs, and cheeks lighter, usually with buffy or pinkish tinge near contact with white of underparts; ears brownish gray, usually a small whitish spot below ear; under parts white, fur basally gray except on throat, breast, inguinal region, and sometimes midline of belly where white to base; tail bicolor, dark gray or blackish above, pure white below; feet white.

Skull: large and robust for the species; rostrum heavy, strongly arched at base; zygomatic arches wide; frontal region broad and moderately channeled; braincase wide and arched; nasals wide anteriorly, lateral margin concave or straight, more strongly tapered posteriorly; dorsal branches of premaxillaries extending 1.0 to 2.2 mm posterior to nasals; supraorbital ridges sharp-angled, sigmoid in dorsal aspect; temporal ridges prominent, diverging posteriorly to line of widest separation near posterior margin of parietals, then turning inward with abrupt angle on parietals; interparietal about two thirds as long as wide between temporal ridges, posterior margin straight or convex; external occipital tubercle absent; dorsal margin of foramen magnum deeply concave or notched; incisive foramina spindle-shaped; anterior palatal spine short, thin, shallow at base and pointed at tip; septum separated from anterior palatal spine by short, narrow maxillovomerine notch; posterior margin of bony palate variably concave; interpterygoid fossa highly variable in shape and width, lateral margin not sharp-rimmed; sphenopalatine vacuities widely open; bullae moderate in size, flattened laterally; upper incisors large, enamel yellow-orange; molars large; anterointernal fold of M1 deep for the species, cutting about half way, or a little farther, across first enamel loop.

A subadult (DM 3240) taken on 29 May at Furnish Canyon: total length 231 mm; length of tail 94 mm; postjuvenal molt nearly completed; worn, thin juvenal pelage on head and neck and between shoulders; elsewhere new subadult pelage, which is long, dense and smooth; upper parts gray with heavier overlay of black than in adults from one mile northwest of Higbee, general effect being dark gray (M and P: 40 A 2; R: Deep Mouse Gray); lower part of sides suffused with cream; skull small, smooth and fragile; cranial sutures open; posterior margin of palate convex and slightly bilobed; anterointernal fold of M1 cutting more than half way through first enamel loop. The size, pelage, and condition of skull indicate that the individual was a young subadult with, perhaps, more advanced molt than is usual for an animal of this size; but the pattern of wear on the upper molars is that of a young adult. The dentine of M3 on each side is continuous, enclosing no enamel islands, and surrounded by one continuous band of enamel. Such a condition is ordinarily not attained until the wood rat is nearly full grown.

Comparisons.—*N. albigula warreni* is the grayest of known subspecies of white-throated wood rats. It differs cranially also from *N. a. albigula, N. a. laplataensis,* and *N. a. brevicauda* in more angular configuration of temporal ridges, narrower maxillovomerine notch, and deeper anterointernal enamel fold of M1.

Remarks.—Of the ten specimens from one mile northwest of Higbee, on which the above description of *N. albigula warreni* (see p. 298) is based, only four skins were saved, representing different color variants. The grayest of the four skins is, to my eye, indistinguishable from each of several skins of *N. micropus canescens* from Baca County. The ten skulls vary greatly in the width of the nasals, size of the sphenopalatine vacuities, and the length, width, and shape of the interpterygoid fossa, which in some skulls extends as far forward as the anterior face of M1. The margin of the fossa on each side may be a continuous rim from the posterior border of the palate to the pterygoid processes, or it may be interrupted by a flattening out of the palatine rim at the widest point of the fossa. An adult male (KU 37107) has a fossa as wide as in some *N. m. canescens.* The anterior palatal spine may taper to only a fine point barely touching the septum, or may be a blade as wide, at its contact with the septum, as it is at its base. The anterointernal fold of M1 varies in depth, in some specimens cutting more than half way across the first enamel loop, and in others a little less than half way. This development of the fold is approximately the same as in *N. micropus canescens* and intermediate between the degrees of development in *N. mexicana fallax* and *N. albigula albigula.* Considering all specimens of *N. a. warreni* examined, a few had such deep anterointernal folds as to be indistinguishable from *N. m. fallax,* on this character. The first division in Goldman's key to the species and subspecies of the subgenus *Neotoma* (Goldman, 1910: 16) is based on the depth of the anterointernal fold of M1. If his key is followed to identify wood rats from southeastern Colorado, nearly half of the specimens of *N. a. warreni* will be thrown somewhere in the *mexicana* group.

The skins of nine topotypes from Gaume's Ranch, collected by E. R. Warren in May 1905, were salted. They nearly match the brownest of the four skins, not so treated, collected in May 1950, one mile northwest of Higbee. The nine topotypes were not used in this study for description of the subspecies because of the possibility of alteration of the original colors by the salt treatment. The skulls of the topotypes vary in the shapes of the nasals and frontals. The dorsal branches of the premaxillaries extend from 0.7 to 2.6 mm posterior to the nasals. The greatest variability occurs in the shape of the interpterygoid fossa. Among the topotypes, ERW 735 has a V-shaped interpterygoid fossa which extends forward to a line joining the posterior margins of the M2s; ERW 737 has a nearly square fossa; ERW 738 has an evenly rounded fossa with a slight notch in the palatal margin; and MVZ 7044 has a widely spreading, nearly hexagonal fossa with a broad, blunt point on the palatal margin, much as in *N. micropus*. ERW 738 has, also, a slightly forked anterior palatal spine not in contact with the septum. ERW 745, an old adult male, has on each M1 a distinct supernumerary anterior enamel fold in the anterior face of the first enamel loop, in addition to the regular anterointernal fold which is shallow on each side. The extra fold on the right M1 is narrow and cuts nearly half way through the loop. The extra fold on the left M1 is a shallow notch.

An adult male (DMNH 2785) from Rock Crossing, thirty miles south of La Junta, taken on 15 July 1936, has the dorsum more brownish (M and P: Buckskin, 14 A 6; R: Wood Brown) than specimens from one mile northwest of Higbee and from the type locality. On the venter the area of fur that is white to the base is more extensive, covering a width of 32 mm on the belly. The skull does not differ from those from one mile northwest of Higbee.

Two adults from Jimmie Creek, collected in May, 1914, are only a little less brownish dorsally than the specimen from Rock Crossing and are more heavily streaked with black on the back. The skulls are like those from one mile northwest of Higbee.

The only skin from Regnier (DM 1289, skull not found), taken in May, 1914, resembles in color the adults from Jimmie Creek. Skulls-only were saved by me of 21 specimens collected 30 May to 2 June 1951 at three localities as follows: Regnier (5 specimens), 2 miles north of Regnier (10 specimens), and 7 miles west and 2 miles north of Regnier (6 specimens). The skins, in the flesh, were not recognizably different in color from skins from one mile northwest of Higbee, although there were perhaps more of the brownish gray individuals and fewer bluish gray ones. The combined series of 21 skulls (9 males and 12 females) from the three localities includes 13 adults, 6 subadults, and 2 seniles. Seven of the 21 skulls do not differ from those from one mile northwest of Higbee but vary as much as the latter in width and shape of the interpterygoid fossa, depth of the anterointernal fold of M1, and in width of the anterior palatal spine at its tip or junction with the septum. Ten of the 21 skulls differ in at least one feature resembling *N. micropus canescens.* Two of the ten resemble *canescens* in two characters. To summarize these variations: Five of the 21 skulls have a point or projection on the posterior margin of the palate, and one has a convex margin. Two have a wide interpterygoid fossa as in *canescens,* but not exceeding the great range of variation in this feature shown by the series of *warreni* from Higbee. One has massive molars. One has the supraorbital region arched. One has the temporal ridges most widely separated on a line near the middle of the parietals. One has the zygomatic arches wide posteriorly. Four skulls differ from those from Higbee and from those of *N. m. canescens* in having the anterior palatal spine free from the septum (maxillovomerine notch open anteriorly).

An adult female (KU 41079) from Regnier differs from adults from one mile northwest of Higbee in the more strongly inflated braincase, pointed posterior ends of incisive foramina, large point or projection on the posterior margin of the palate, and narrow interpterygoid fossa having widely depressed lateral margins.

An adult female (KU 41074) from two miles north of Regnier is the only specimen of *N. albigula* examined having a deeply forked anterior palatal spine indistinguishable from the forked spine of *N. floridana.* A few *N. albigula* and *N. micropus* have been seen with a slightly forked tip of the palatal spine, but no other distinctly forked spine has been seen except in the species *floridana,* of which it is diagnostic. The skull of KU 41074 also differs from those from one mile northwest of Higbee in having the zygomatic arches more widely spreading posteriorly, in this respect resembling *N. m. canescens.* By all other characters it clearly belongs to *N. a. warreni.*

Of the 41 skins at hand for comparison, 3 were taken in June, 1 in July, 3 in September, 1 in December, 1 in February, and the rest in the spring. The only skin in dense unworn pelage is a young adult female taken on 12 December 1892, at Trinchera. This specimen and the old adult male taken on 14 February 1937, 20 miles east of Walsenburg, are a little more yellowish gray than the series from one mile northwest of Higbee, described above, and the series of nine topotypes. The specimen from 20 miles east of Walsenburg has narrow nasals, narrow frontals, a short broad interparietal, and a wide maxillovomerine notch, in comparison with skulls from one mile northwest of Higbee. The specimen from Trinchera has a smaller skull, narrower and lighter zygomatic arches, a narrower frontal, weaker temporal ridges, and smaller bullae.

One of the three skulls-only from nine miles southwest of Walsenburg, 6600 feet elevation, has the anterior palatal spine tapered to a fine point free from the septum. The ventral edge of the septum forms a nearly straight line. The other two skulls have the tip of the spine in broad contact with the septum.

An adult female (KU 37102) from two miles east of Wetmore, 5700 feet elevation, differs from adults from one mile northwest of Higbee in wider zygomatic arches, temporal ridges bending inward less abruptly, and the posterior margin of the bony palate with an asymmetrical projection.

An adult male (KU 37120) from 11 miles north and 8 miles east of Branson, 5600 feet elevation, taken on 25 May 1950, has an extraordinarily inflated braincase that is smooth and nearly round in dorsal aspect and strongly arched in lateral aspect. The temporal ridges are barely traceable. The greatest breadth of braincase, measured at the upper base of the zygomatic arches, is 21.0 mm. The depth of braincase, measured longitudinally from the basisphenoid to the sagittal line, is 14.6 mm. Two normal adult skulls of the same size (KU 37117 male and KU 37108 female) from one mile northwest of Higbee measured, respectively: breadth of braincase, 18.2 and 17.8 mm; depth of braincase, 11.9 and 12.2 mm. The abnormally inflated skull resembles *N. a. warreni* in all diagnostic characters. Its age, as indicated by tooth wear, is second year adult.

Three adults (KU 37111 ♀, KU 37119 ♂, and KU 37114 ♀) from one mile northwest of Higbee were excluded from the series used for description of the subspecies (see p. 298), because each has two characters diagnostic of *N. micropus*. In all other characters they resemble *N. albigula warreni*. KU 37111 is light brownish gray, browner than any *N. micropus*. Its skull is arched in the supraorbital region, and the temporal ridges curve smoothly (not angularly) inward on the parietals, as in *N. micropus canescens*. KU 37119 (skull only) is also arched in the supraorbital region, and the braincase is flattened (not arched) above, as in *N. micropus canescens*.

The skin of KU 37114 is gray, heavily overlaid with black, with a faint buffy tinge on the lower sides. It might pass for either *N. albigula warreni* or *N. micropus canescens.* Its skull has a short, thin, deep anterior palatal spine broadly in contact with the vomer, and the septum is virtually intact as in *N. micropus,* there being only a narrow slit for a maxillovomerine notch. This is the only skull of *N. albigula warreni* examined that does not have a distinct maxillovomerine notch in the septum. These three specimens may result from introgressive hybridization between *N. a. warreni* and *N. m. canescens.* On the balance of diagnostic characters, they are referred to *N. albigula warreni.*

Two out of six skins from ten adult *N. a. warreni* collected in March and May at Two Buttes peak and Two Buttes Reservoir are nearly clear bluish gray (Jack Rabbit, 39 A 2), indistinguishable by color from many specimens of *N. micropus canescens.* One of the six is darker middorsally than any skin from one mile northwest of Higbee. The other three fall within the range of color variation shown by skins from one mile northwest of Higbee. The skin taken in March has longer fur than those taken in May. The skulls of the ten adults (including four skulls-only) from Two Buttes peak and Two Buttes Reservoir resemble, in most features, skulls of adults from one mile northwest of Higbee, but each of the ten differs in at least one respect. Three of the ten skulls differ in having the posterior margin of the palate convex. Two of the seven with a concave palatal margin have on the margin two low knobs divided by a median ventral sulcus. Two of the ten differ in that the palatal margin bears a point deflected dorsally into the narial passage. Three have a larger maxillovomerine notch open anteriorly and separating the anterior palatal spine from the vomer. One of the ten has the tip of the anterior palatal spine slightly divided and barely touching the vomer.

The oldest skull (KU 37126 ♀) of the ten from Two Buttes peak and Two Buttes Reservoir (or, indeed, of any skull of *N. a. warreni* examined) is larger than the others and has a more flattened cranium and more pronounced temporal ridges than any of the younger skulls. It has a wider interpterygoid fossa resembling that of *N. micropus canescens,* and is one of the four mentioned above having a larger maxillovomerine notch. The upper molars are so extremely worn that half of the enamel folds have been obliterated. The lower molars lack any trace of an enamel fold. The pulp cavities are exposed in the roots of both M2s and both M3s, and the two roots of the right M2 have broken apart. The occlusal surfaces of upper and lower molars curve dorsally anteriorly, as seems to be usual with senile wood rats of other species.

Two adults (KU 37125 ♂ and DM 5653 ♀) included in the ten specimens described above from Two Buttes peak and Two Buttes Reservoir have temporal ridges intermediate in form between *N. a. warreni* and *N. m. canescens* (recurving less abruptly than in *warreni* and not so far back as the posterior margin of the parietals). KU 37125 has also an irregularly convex palatal margin and a wide interpterygoid fossa.

Three out of 11 specimens (KU 37132, DM 4823, and DM 5654) from Two Buttes Reservoir and Two Buttes peak have, each, three or more characters normally found in *N. micropus canescens* and not in *N. albigula warreni.* They seem to be hybrids more nearly resembling *warreni* and representing, probably, a generation subsequent to F_1, perhaps resulting from a backcross of a hybrid with a *warreni.*

An old adult male (DM 5654) from Two Buttes Reservoir was not included in the ten specimens described above, because of its marked cranial differences. The skin is light gray with a buffy line on the lower sides. The skull strongly resembles *N. micropus canescens* in general form, owing to the arched supraorbital region, low braincase, and gradually recurving parietal ridges. The molars are massive as in *canescens,* and the zygomatic breadth intermediate between *canescens* and *N. a. warreni.* The posterior palatal margin is nearly square with two small, irregular points. It resembles *warreni* in the large maxillovomerine notch open anteriorly, the small slender-pointed anterior palatal spine, absence of an external occipital tubercle, the notched supraoccipital margin of the foramen magnum, the wide interparietal between temporal ridges, and the wide (but not extreme) interpterygoid fossa. I consider this specimen a hybrid between *N. a. warreni* and *N. m. canescens,* but since the balance of characters leans more in favor of *N. a. warreni* I refer it to *warreni,* as a matter of practical convenience.

One adult from Two Buttes Reservoir (KU 37132 ♂), included in the ten specimens described above, differs from adults from one mile northwest of Higbee and approaches *N. micropus canescens* in having the supraorbital region slightly arched, the posterior palatal margin with a point deflected somewhat dorsally, and the maxillovomerine notch almost completely closed by the deep anterior palatal spine. Other cranial characters and the pelage are as in *N. albigula warreni.* The baculum has the long slender constricted shaft, the distinct distal head, and the short light base typical of *N. albigula.*

An adult (DM 4823 ♂) from Two Buttes Reservoir, included in the ten specimens described above, has the supraorbital region arched, zygomatic arches wide posteriorly, and massive molars, as in *N. micropus canescens.* Other cranial characters and pelage are typical of *N. albigula warreni,* as shown by specimens from one mile northwest of Higbee.

Nearly every one of the characters most reliable for distinguishing *N. a. warreni* from *N. m. canescens* has been found in a few specimens (perhaps hybrids) that, on the whole, most resemble the other species. I know of no single feature by which all specimens of the two species in Colorado can invariably be separated. The form of the baculum may be completely distinctive for each of the species; however, bacula of only 2 adult *canescens* and 11 adult *warreni* were preserved and mounted from southeastern Colorado. Only one baculum is from a specimen (KU 37132) described in this study as a hybrid, referred for practical convenience to *N. a. warreni,* and the baculum is typical of *warreni.* A greater number of bacula would be needed to obtain evidence for or against hybridization from this structure.

The external occipital tubercle in *N. micropus canescens* is an inconspicuous but reliable character not clearly developed on any specimen referred to *N. albigula warreni.* It is a small projection which is sharply pointed in old age, but no more than a short, low crest in subadults. In spite of its small size, the external occipital tubercle is a useful character for distinguishing adults in southeastern Colorado; but a cursory survey of specimens of *N. albigula* and *N. micropus* from widely separated parts of the southwestern United States and Mexico leads me to believe that the presence or absence of the tubercle is not a reliable distinction between the two species in all parts of their ranges. There seems to be some geographic variation in the occipital region in both species, as well as much change with age.

Other features highly reliable for distinguishing *N. a. warreni* from *N. m. canescens* in Colorado are the arching of the supraorbital region, the presence or absence of a maxillovomerine notch, and the configuration of the parietal ridges. But each of these features in one or more specimens of *warreni* and *canescens* fails to agree with the determination made from the majority of characters.

Numerous features ordinarily differ between *N. a. warreni* and *N. m. canescens,* but not infrequently resemble the condition in the opposite species. Among these features are the arching or flattening of the braincase, the position of greatest separation of the parietal ridges, the zygomatic breadth, the shape of the dorsal margin of the foramen magnum, the width (in the median plane) of the anterior palatal spine, the shape of the posterior margin of the bony palate, the shape of the interpterygoid fossa, and the size of the molars (particularly M1). Of these, the shape and breadth of the interpterygoid fossa is unusually variable in *warreni* but nearly constant in *canescens.* The same may be said for the color of the pelage. The absence of a point on the posterior palatal margin seems to be a more frequent variation in *canescens* than the presence of the point in *warreni;* and the point, when present in the latter, is usually smaller and/or less symmetrical.

To summarize briefly the foregoing morphologic and geographic facts: Normal individuals (showing no intermediate or opposite characters) of *N. albigula warreni* and *N. m. canescens,* as well as specimens with a mixture of characters, are at hand from the vicinity of Two Buttes Reservoir. From Monon only *canescens* and possible hybrids are at hand. From Gaume's Ranch and the vicinity of Higbee only *warreni* and possible hybrids are available, although a *canescens* is recorded from within five miles of Higbee, at 18 miles south of La Junta. At Furnish Canyon and localities in the vicinity of Regnier, both species are present; and most of the specimens clearly are of one species or the other, although a few specimens of each species have one or two characters of the opposite species.

It seems to me that occasional hybridization takes place between *warreni* and *canescens* in the vicinity of Two Buttes Reservoir, and possibly at other localities. The evaluation of specimens showing evidence of mixed ancestry suggests a pattern of hybridization resembling that in the red-eyed towhees of Mount Orizaba, described by Sibley (1950: 160-162). As in the towhees of Mount Orizaba, all of the wood rats have characters predominantly of one species or the other, none being sufficiently intermediate to be regarded as an F_1 hybrid from the crossing of pure parental species. They represent, rather, various degrees of intermediacy between the probable phenotype of an F_1 hybrid and one or the other "pure" species. Such a distributional pattern of hybrid characters might be expected in a sample population if the F_1 hybrids are produced only occasionally and do not suffer reduced fertility. The chances of obtaining an actual F_1 hybrid would be slight, compared with the chances for various lesser intermediates of subsequent generations.

The occurrence of mixed characters at Monon and in the vicinity of Higbee may be due solely to introgressive hybridization spreading out from Two Buttes Reservoir. The scarcity of mixed characters farther south near Furnish Canyon and Regnier, in spite of the presence of both species there, speaks in favor of introgressive hybridization rather than local hybridization along the Colorado-Oklahoma line. For a discussion of the ecological evidence bearing on hybridization, see the section on competition and ecologic divergence (pp. 531 to 537).

Another possible explanation of the relationship between *N. a. warreni* and *N. m. canescens* in southeastern Colorado might be intergradation. Strong evidence against this is: (1) the presence of typically normal individuals of both species at the same localities, including Two Buttes Reservoir, along with specimens having various mixtures of characters; (2) the absence of any morphologically and geographically intermediate population forming a transition between the two species; (3) the extraordinary range of variation shown by the populations in question, greatly exceeding the variation of either species at localities outside of Colorado; and (4) the sympatric distribution of the two species throughout an extensive north-south range in New Mexico, Texas, and Coahuila.

Other alternative explanations might be: (1) that the "abnormal" characters ordinarily found in the opposite species have persisted as scarce or recessive alleles inherited from some mutually ancestral population and retained in the populations of both species in Colorado; (2) that the "abnormal" characters have appeared, subsequent to the divergence of the two species, as mutant alleles identical with those "normal" to the opposite species; and (3) that none of the characters discussed is diagnostic for either species, and that more detailed study of larger series of both species would reveal some completely constant and distinctive, perhaps inconspicuous, characters for each.

However, whether the characters concerned be due to mutant alleles or the persistence of identical alleles, or whether they be of no taxonomic significance, none of these alternative explanations accounts for the present distribution and frequencies of the characters. The hypothesis of hybridization does make this pattern of variation at least partly understandable.

It should be emphasized, in conclusion, that hybridization is suggested here only as a tentative explanation that needs to be tested by much more evidence. Careful morphological and ecological studies of *Neotoma albigula* and *N. micropus* of a scope including their entire ranges would undoubtedly throw much light on the question.

Whatever may prove to be the correct interpretation of the relationship between *N. a. warreni* and *N. m. canescens* in southeastern Colorado, it is evident that the two species are more similar in that area than in other parts of their ranges. Quite apart from any hybrid or intermediate individuals, the subspecies *warreni* is characterized by several traits intermediate between those of *N. a. albigula* and *N. m. canescens.* The stocks of *albigula* and *micropus* in Colorado probably have diverged from a common ancestral stock and are less effectively isolated reproductively than the populations of the two species farther south.

In his account of "*Neotoma fallax*" Cary (1911: 118) states, in part, "At Walsenburg and Badito, in Huerfano County, . . . these rats often construct their nests [houses] entirely of the spiny branches of tree cactuses . . ." Since no specimen from either locality is known to me, I judge that Cary attributed the cactus houses to the only species he believed to occur in the area. However, of the many dens of *N. mexicana fallax* examined in the present study, none was found constructed of tree cactus. The houses studied, made of tree cactus joints in eastern Colorado, were made by *N. albigula warreni, N. micropus canescens,* and *N. floridana campestris.* Since *warreni* is the only one of these three known to occur in the area concerned, the houses mentioned by Cary probably were constructed by *warreni,* not *fallax.* The two localities are indicated on the map, Figure 4, as *18* and *19.*

Specimens examined.—Total 81, from Colorado as follows: (*1*) 2 mi. E Wetmore, 5700 ft., Custer Co., 1; (*3*) 20 mi. E Walsenburg, "Huerfano Co." [?], 1 (DMNH); (*4*) 9 mi. W junction Purgatoire [= Picketwire, = Purgatory] and Chacuaco [= Chaquaqua] creeks, 3 (MVZ); (*5*) 6 mi. NW Higbee, 4550 ft., 2; (*6*) 1 mi. NW Higbee, 4200 ft., 12; (*7*) Rock Crossing, 30 mi. S La Junta, *in* Las Animas Co., 1 (DMNH); (*7*) 10 mi. N Officer, 1 (DMNH); (*8*) Irwin's Ranch, T. 29 S, R. 52 W, 5000 ft., 2 (ERW); (*9*) Gaume's Ranch, Shell Rock Canyon, 4600 ft., sec. 21, T. 28 S, R. 50 W, Baca Co., 11 (2 BSC, 8 ERW, 1 MVZ); (*10*) Two Buttes Creek, 14 mi. N Springfield, 4300 ft., 3 (TCWC); (*11*) Two Buttes peak, 4500 ft., Prowers Co., 4; (*11*) 1 mi. N Two Buttes Reservoir, 4350 ft., Prowers Co., 1; (*11*) Two Buttes Reservoir, 4250 ft., Baca Co., 7 (3 DMNH); (*12*) 11 mi. N and 8 mi. E Branson, 5600 ft., 1; (*13*) Furnish Canyon ["Furnace Canyon" on skin labels; approximately 37° 02′ N, 103° 02′ W], Baca Co., 2 (DMNH); (*13*) 7 mi. W and 2 mi. N Regnier, 4550 ft., 6; (*14*) Regnier, 4500 ft., 37° 00′ N, 102° 50′ W, Baca Co., 6 (1 DMNH); (*14*) 2 mi. N Regnier, 4575 ft., 10; (*14*) Jimmie Creek [= Sand Canon, on U. S. G. S. Topo. Map, Springfield Quadrangle; approximately 37° 03′ N, 102° 49′ W], 3 (DMNH); (*15*) Trinchera, 1 (DMNH); (*16*) 7 mi. E and 1 mi. S Trinidad, 3; (*17*) 9 mi. SW Walsenburg, 6600 ft., 3.

Additional records.—(*2*) near junction Huerfano and Cucharas rivers, Pueblo Co. (F. W. Miller, 1931: 432); (*18*) Badito (see above, this page); (*19*) Walsenburg (see above, this page).

Neotoma micropus Baird

Gray wood rat

Neotoma micropus Baird, Proc. Acad. Nat. Sci. Philadelphia, 7: 333, April 1855.

Distribution.—Plains and lowlands of eastern New Mexico and western Texas, north to the Arkansas River in southeastern Colorado and Kansas, and south into San Luis Potosi.

Diagnosis.—Upper parts gray or brownish gray; throat, breast and inguinal region pure white to base of hairs; skulls robust, strongly arched and channeled in frontal region; temporal ridges projecting prominently over orbits, flaring widest on parietals, converging gradually toward interparietal; length of interparietal nearly as great as width between temporal ridges; anterior palatal spine pointed; maxillovomerine notch absent; posterior margin of palatal bridge with prominent point, or occasionally concave or square; interpterygoid fossa widely rounded laterally; sphenopalatine vacuities widely open; upper incisors wide and heavy.

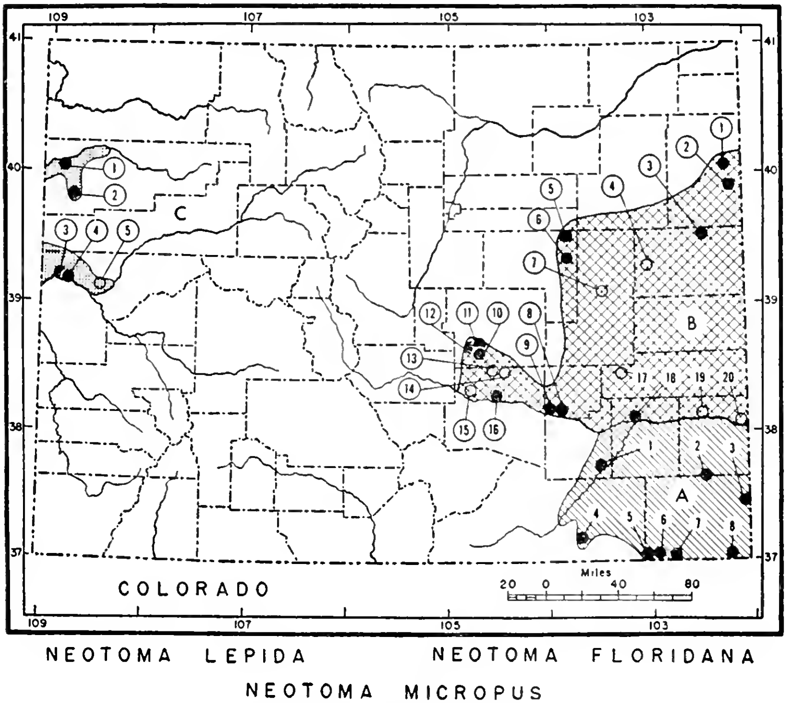


Fig. 5. Distribution of three species of *Neotoma*: A, *N. micropus canescens*; B, *N. floridana campestris*; C, *N. lepida sanrafaeli*. Symbols: solid circles, specimens examined; hollow circles, additional records. Numbers refer to localities listed under accounts of subspecies (see pp. 315, 318, and 332).

Comparisons.— *Neotoma micropus* is, on the average, grayer than any other kind of wood rat in Colorado and can be distinguished from all except *N. floridana* by absence of a maxillovomerine notch in the septum. From *N. floridana* it can be distinguished by the single-tipped (unforked) anterior palatal spine, wider sphenopalatine vacuities, and pointed posterior margin of palatal bridge.

Some specimens of *N. albigula warreni* are as gray as *N. micropus canescens* and indistinguishable from it by pelage or external measurements. Nevertheless, the skulls of *N. micropus* are distinguishable from those of *N. albigula* of whatever subspecies by the more arched supraorbital region and absence of a maxillovomerine notch. Skulls of *canescens* are also distinguishable from *warreni* by the curved (in contrast to angular) parietal ridges, external occipital tubercle, shallower supraoccipital margin of foramen magnum, wider interpterygoid fossa, wider zygomatic arches, and heavier molars; but these characters, individually, are not consistently reliable. The baculum proved useful in distinguishing adult males of these two species. *N. micropus* has a thicker less constricted shaft and a heavier more bell-shaped base than *N. albigula.*

Neotoma micropus canescens Allen

Neotoma micropus canescens Allen, Bull. Amer. Mus. Nat. Hist., 3: 285, 30 June 1891; Goldman, N. Amer. Fauna, 31: 28, 19 October 1910; Cary, N. Amer. Fauna, 33: 115, 17 August 1911; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 210, 1942.

Neotoma micropus, Warren, Colorado Coll. Publ., Gen. Ser. no. 19, p. 248, January 1906; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 109, 1910; Goldman, N. Amer. Fauna, 31: 26, 19 October 1910, part.

Type.—AMNH no. 3030/2350, adult male, skin and skull; from North Beaver [= North Canadian] River, Indian Territory [Oklahoma], near the boundary line between the Indian Territory and New Mexico; collected 20 October 1889 by Richardson and Rowley.

Range.—Outside of Colorado the subspecies occurs in western Texas, Coahuila, the low valleys of New Mexico, and the "panhandle" of Oklahoma. In Colorado it has been found only south of the Arkansas River and east of the 104th meridian. (See map, Fig. 5).

Diagnosis.—Pelage long and soft for the species; upper parts light bluish gray; cheeks and sides light gray, rarely suffused with buffy.

Description.—Adults in partly worn pelage taken late in May at Furnish Canyon: size medium; tail about 70 per cent as long as head and body; hind feet and ears of medium length for the genus. Pelage: short to moderately long; tail covered with short hairs; longest vibrissae 65 mm. Color: upper parts light bluish gray overlaid with black or dusky, general effect being Jack

Rabbit (39 A 2) to near Rail (39 A 5; R: Neutral Gray to Deep Neutral Gray); sides and legs lighter (Slate-Gray; R: near Smoke Gray); ears brownish gray, usually a small whitish spot below ear; underparts white, fur basally gray except on throat, breast, and inguinal region where white to base; tail bicolor, black or dusky above, white or light gray below; feet white.

Skull: robust and angular; rostrum large; zygomatic arches widely spreading posteriorly; frontal region strongly arched and channeled; braincase wide, flattened above in old adults; nasals slightly flaring anteriorly, lateral margins nearly parallel, strongly tapered posteriorly; dorsal branches of premaxillaries extending 0.6 to 1.8 mm posterior to nasals; supraorbital ridges elevated, forming sharp rims over orbits, sigmoid in dorsal aspect; temporal ridges pronounced, diverging gradually posteriorly, most widely separated on line through middle of parietals, curving smoothly inward onto interparietal; interparietal one half to two thirds as long as wide between temporal ridges, posterior margin convex or angular; external occipital tubercle present; dorsal margin of foramen magnum shallowly concave or straight; incisive foramina long, spindle-shaped; anterior palatal spine short, thin, deep at base and pointed at tip; septum intact (maxillovomerine notch absent); posterior margin of palate usually pointed, interpterygoid fossa widely rounded or hexagonal, lateral margin not sharp-rimmed; sphenopalatine vacuities widely open; bullae small; upper incisors large, enamel yellow-orange; molars wide; M1 massive, anterointernal fold shallow or cutting about half way across first enamel loop.

A subadult taken in May at Cimarron River: total length 255 mm, tail 95 mm, hind foot 3 mm; molting on back and sides; old, dark gray juvenal pelage on back short, thin and fuzzy; new subadult pelage on sides lighter gray, short and smooth; tail thinly haired with extremely short gray hairs, scales showing through.

An immature taken in April at Monon: total length 216 mm, length of tail 80 mm, length of hind foot 35 mm; juvenal pelage long and rather thin; upper parts darker (M and P: African, 8 E 8; R: near Fuscous Black) than in spring adults; tail shorter-haired, less distinctly bicolor and lighter gray above.

Comparisons.—Specimens of *Neotoma micropus canescens* from Colorado differ from specimens of *Neotoma m. micropus* from south central Kansas (Kiowa and Barber counties) in smaller average size, shorter tail, and lighter color. No consistent cranial differences were found. Colorado specimens of *N. m. canescens* differ from specimens of *N. m. micropus* from Brownsville, Texas, in grayer (less brownish) color, heavier rostrum, wider nasals, wider zygomatic arches, and narrower frontal region.

Remarks.—In his original description of *canescens*, Allen (1891) did not designate a holotype. But Goldman in his revision of the genus *Neotoma* (1910: 28) referred to AMNH 3031/2351 female, as the type. On the basis of published information alone, Goldman's reference might constitute designation of a lectotype. However, a different specimen, AMNH 3030/2350 male, bears a type label. Mr.

G. G. Goodwin of the American Museum of Natural History has kindly offered (*in litt.*) this explanation of the circumstances: Dr. Allen tied his type label which specified male, adult, on AMNH 3030/2350. Possibly in error Allen marked AMNH 3031-2351, a female, as the type in the catalogue and on his personal separate, but both entries were changed later in favor of the labeled type. Probably Goldman had one of the separates on which Allen had written "type" opposite number 3031/2351. Goodwin expressed his personal confidence that Allen selected number 3030/2350 as the type and wrote this number on the type label himself. In fact, this specimen is the only one in the series with the identification in Allen's handwriting.

I agree with Goodwin and regard AMNH 3030/2350, male, as the valid holotype of *N. m. canescens.*

Two topotypes (AMNH 3031/2351 and 3032/2352) have a distinct point on the posterior margin of the bony palate, as is usually present in this species. But the type (AMNH 3030/2350) has a smoothly concave posterior margin of the palate.

No specimens of *N. micropus canescens* in fresh adult pelage are available from Colorado, all, unfortunately, having been collected in the spring.

The largest series of *canescens* at hand from Colorado consists of ten specimens (adults and subadults) from Furnish Canyon, which is about 25 miles north of the type locality. Eight of these ten have a distinct point, or projection, on the posterior margin of the bony palate, and two have no point, the margin being nearly square. One of the ten skulls has a minute point on each side of the tip of the anterior palatal spine, but the spine is not really forked. The palatal spines of the other nine skulls are all single-tipped. These features do not change with age.

Two old adults (DM 5651 ♂ and DM 5652 ♀) collected on 11 March 1949 at Two Buttes Reservoir show clearly the characters diagnostic of *N. micropus canescens.* Some of the diagnostic characters of the species are more salient than in any of the adults from Furnish Canyon, owing to the more intense expression of these characters with increasing age. DM 5651 is lighter gray with less blackish overlay than adults from Furnish Canyon, and DM 5652 is more slate gray. The skulls of both differ in larger size, heavier rostrum and zygomatic arches, wider nasals, more arched frontal region, more prominent supraorbital and temporal ridges, and more flattened braincase. These cranial differences are all due to age. In addition, DM 5651 shows individual difference in the position of the point on the posterior margin of the bony palate, projecting dorsally into the narial passage, and the persistence of a complete median frontal suture. The latter peculiarity was not present in any of the other 48 skulls, young or old, of this race examined. I do not recall seeing a complete median frontal suture in any other adult wood rat of any species.

A young adult male (KU 37129) from one mile north of Two Buttes Reservoir taken on 10 May 1950, has nasals unusually wide anteriorly, the posterior palatal margin concave, and bullae narrower than those of adults from Furnish Canyon and Two Buttes Reservoir. Although KU 37129 has a normal pattern of wear on the right M3, the left M3 seems not to have reached the normal adult condition. The anterior enamel loop is a closed ring separated from the middle lobe by the junction of the unusually deep inner fold and anteroexternal fold.

An old adult female and a subadult female from the Cimarron River have the posterior margin of the palate concave in ventral aspect but with a small point projecting dorsally into the narial passage in posterior aspect. The interpterygoid fossa of the old adult extends forward to a line joining the posterior roots of the M2s. Tooth wear in this rat has taken place not only on the occlusal surfaces, but on the vertical surfaces between adjoining molars, both above and below. Between M2 and M3 on each side, less than half of the posterior lobe of M2 has been worn away, and more than half of the anterior lobe of M3. Somewhat less has been worn away between M1 and M2.

Four skulls from 7 miles west and 2 miles north of Regnier, Colorado, resemble skulls from Furnish Canyon but show slight differences. Two of the four skulls have the supraoccipital margin of the foramen magmum more deeply concave. A third skull has the enamel worn through on the adjoining vertical surfaces of the three left upper molars. A damaged skull from Regnier, Oklahoma, shows even heavier wear between the adjacent upper molars, extending as much as half way through the dentine of adjacent lobes, but does not differ from skulls from Furnish Canyon in other respects. A single skull from three miles southeast of Regnier, Oklahoma, differs in having the posterior palatal margin straight, not pointed.

(Regnier, Colorado, and Regnier, Oklahoma, are separate localities about one half mile apart and separated by the Colorado-Oklahoma state line. According to Mrs. Ed. Tappe, wife of the manager of the Willson Ranch at Regnier (verbal communication, 1951), the Regnier Post Office was at the ranch headquarters on Gallinas Creek in Colorado, until the old house burned down (perhaps 50) years ago. The Regnier Post Office then was transferred to the new ranch headquarters at the present site on Pat Creek in Oklahoma.)

Three second year adults (skulls only) from 11 miles north and 8 miles east of Branson, 5600 feet elevation, are of nearly the same age but differ markedly in size and cranial characters. All three have curving (rather than angular) temporal ridges, no maxillovomerine notch, an external occipital tubercle, a point on the posterior edge of the palate, and a wide interpterygoid fossa; and on these characters the three specimens are referred to *N. m. canescens*. The skull of the largest (KU 37122 ♀) closely resembles those from Furnish Canyon (see p. 311) but is not so large. The skull of KU 37124 female is shorter and less strongly ridged than that of KU 37122, with the frontals wider, supraorbital borders less elevated, braincase more arched, temporal ridges more widely separated, interparietal wider, tip of anterior palatal spine slightly forked, sphenopalatine vacuities narrower, and bullae smaller. Many of these characters are ordinarily indicative of younger age; yet on the basis of the amount of wear on the molars, the ages of these two skulls are barely distinguishable. The third adult (KU 37121 ♂) has the smallest external measurements and much the shortest and smoothest skull. The frontals are of the same width and less elevated than those of the second (KU 37124), the braincase more inflated dorsally, the temporal ridges equally separated, the interparietal less wide, the anterior palatal spine single-tipped, the sphenopalatine vacuities wider, and the bullae larger (between KU 37122 and KU 37124 in size). The wear on the molars of KU 37121 indicates it to be only slightly younger than the other two. The only other adult skull that is comparable to KU 37121 and KU 37124 in small size, shape of frontals and temporal ridges, and inflation of braincase is a younger adult female (ERW 595) which is intermediate in basilar length, but wider than either across the zygomata. It is noteworthy that ERW 595 is from Monon, the easternmost locality of occurrence in Colorado, whereas the other two are from the westernmost locality. The differences between these three small skulls and the normal skulls of the same age as described from Furnish Canyon are comparable in kind and greater in degree than the difference between Figures 6 and 7 of Plate IV in Allen (1894).

The skins of five adults (ERW 617, ERW 618, ERW 587, ERW

595, and MVZ 7045) from Monon, collected in April and May, 1905, were treated with salt. They are not so gray as the adults from Furnish Canyon. Four of the 5 adults and 1 subadult (ERW 603) have the posterior margin of the palate concave without any point, thus differing from the Furnish Canyon series, in which 8 out of 10 skulls have a point on the palate. The only skull from Monon (ERW 617) having a point on the palate, has also a slightly, but distinctly, forked anterior palatal spine. The concave palatal margin and the forked palatal spine are suggestive of *N. floridana campestris;* all other characters, however, including pelage, are typical of *N. micropus canescens.* One of the 5 adults from Monon (ERW 587 male) has, besides a concave palatal margin, a short narrow maxillovomerine notch and a deep anterior palatal spine not quite touching the septum. The concave palatal margin and the maxillovomerine notch are more typical of *N. albigula warreni* than *N. m. canescens,* and the skin could pass for either kind. On the basis of most of the diagnostic characters, however, ERW 587 is referable to *N. m. canescens.* One of the five adults from Monon, a young adult female (ERW 595) probably not more than six months old, is smaller than the other four and has a light gray tail. Its skull is shorter and smoother, with zygomatic breadth relatively greater, temporal ridges weaker and more widely separated, braincase more arched, median supraoccipital margin of the foramen magnum notched, and posterior palatal margin concave. Although the last three characters are commonly found in *N. a. warreni,* and not in *N. m. canescens,* I refer ERW 595 to *canescens* on the basis of the smoothly flaring parietal ridges, external occipital tubercle, deep anterior palatal spine, absence of maxillovomerine notch, and breadth of interpterygoid fossa.

Hybridization between *Neotoma micropus canescens* and *Neotoma albigula warreni* may account for the diverse mixture of characters seen in two of the adults from Monon (ERW 587 and ERW 595). For further discussion of hybridization between *canescens* and *warreni,* see *remarks* under *N. a. warreni,* page 302.

Specimens examined.—Total 34, from Colorado except as specified, as follows: (*1*) 18 mi. S La Junta, 1 (BSC); (*2*) 1 mi. N Two Buttes Reservoir, 4350 ft., Prowers Co., 1; (*2*) Two Buttes Reservoir, 2 (DMNH); (*3*) Monon, Bear Creek, J. M. Johnston Ranch, 7 (6 ERW, 1 MVZ); (*4*) 11 mi. N and 8 mi. E Branson, 5600 ft., 4; (*5*) Furnish Canyon ["Furnace Canyon" on skin labels; approximately 37° 02′ N, 103° 02′ W], Baca Co., 10 (DMNH); (*6*) 7 mi. W and 2 mi. N Regnier, 4550 ft., Baca Co., 4; (*7*) Regnier, 4375 ft. [37° 00′ N, 102° 50′ W], Cimarron Co., Oklahoma, 1; (*7*) 3 mi. SE Regnier, 4350 ft., Cimarron Co., Oklahoma, 1; (*8*) Craugh Ranch, Cimarron River, Baca Co., 3 (DMNH).

Neotoma floridana (Ord)

Florida wood rat

Mus floridanus Ord, *in* De Blainville, Bull. Sci. Soc. Philom. Paris, p. 181, December 1818.

N[eotoma] floridana, Say and Ord, Jour. Acad. Nat. Sci. Philadelphia, vol. 4, pt. 2, p. 346, April 1825.

Distribution.—Southeastern United States from South Carolina to central Texas and north in the Great Plains to South Dakota. In Colorado the species reaches its western limit south of Colorado Springs.

Diagnosis.—Size medium to large; ears relatively small; throat and breast white to base of hairs; skull robust, strongly arched; anterior palatal spine forked, not separated from vomer by a notch in septum; posterior margin of palatal bridge concave or notched; sphenopalatine vacuities narrow; auditory bullae small.

Comparisons.—*Neotoma floridana* differs from all other species of wood rats examined in having the anterior palatal spine forked. In addition, it differs from *N. micropus* in less gray color, interorbital ridges straight, posterior margin of bony palate concave or notched, and sphenopalatine vacuities narrower. *N. floridana* differs from *N. albigula* in larger size, skull more robust and arched, interorbital ridges straighter, and septum intact (maxillovomerine notch absent). *N. floridana* differs from *N. mexicana* in larger size, throat and breast white to base of fur, skull more robust and arched, interorbital region wider and more ridged, maxillovomerine notch absent, posterior margin of palatal bridge concave or notched, sphenopalatine vacuities narrower, teeth larger, and anterior median fold of M1 shallow.

Neotoma floridana is widely separated geographically from *N. lepida* and is much larger, with under parts more extensively white and numerous cranial differences. For comparison with *N. cinerea* see page 256.

Neotoma floridana campestris Allen

Neotoma campestris Allen, Bull. Amer. Mus. Nat. Hist., 6: 322, 7 November 1894.

Neotoma floridana campestris, Kellogg, Kansas Univ. Mus. Nat. Hist. Publ. 1, Zool. Ser., vol. 1, no. 1, p. 3, 30 January 1914.

Neotoma floridana baileyi, Warren, Colorado Coll. Publ., Gen. Ser. no. 19, p. 247, January 1906; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 111, 1910; Goldman, N. Amer. Fauna, 31: 24, October 1910; Cary, N. Amer. Fauna, 33: 114, 17 August 1911; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 209, 1942.

Type.—AMNH no. 7765/6742, adult female, skin and skull; from Pendennis, Lane County, Kansas; collected 8 May 1894 by W. W. Granger.

Range.—Outside of Colorado the subspecies occurs in northwestern Kansas and southwestern Nebraska. In Colorado it is found on the Great Plains north of the Arkansas River, ranging north to Wray and west as far as the foothills south of Colorado Springs. (See map, Fig. 5).

Diagnosis.—Upper parts light yellowish brown; white on throat extending up side of neck to base of ear; tail light gray above.

Description.—Adults in unworn pelage taken November to March at Wray: size rather large for the genus; tail about 70 per cent as long as head and body; hind feet rather large; ears relatively small. Pelage: long and smooth; tail covered with short stiff hairs; longest vibrissae 70 mm. Color: upper parts and sides Chamois (11 I 5; R: near Warm Buff), moderately overlaid with black; cheeks and forelegs lighter; side of neck from throat to base of ear white; ears brownish gray; underparts white, fur gray basally except on throat, breast, and inguinal region where white to base; tail bicolor, light gray above, pure white below; feet white.

Skull: robust, strongly arched in frontal region; rostrum long; nasals wide, abruptly tapered posteriorly; interorbital region wide; temporal ridges straight, converging slightly anteriorly, forming sharp rim over orbit, usually bending abruptly inward on parietals; interparietal slightly wider than long between temporal ridges, with obtuse angle on posterior margin; incisive foramina wide, smoothly tapered at each end; anterior palatal spine with forked tip straddling premaxillary septum; septum intact (maxillovomerine notch absent); posterior margin of palatal bridge concave or notched; interpterygoid fossa widely rounded or hexagonal, lateral margin indistinct; sphenopalatine vacuities narrow slits almost closed posteriorly; bullae small; incisors medium; molars large; anterior median enamel fold of M1 shallow.

Adults in worn pelage, taken in summer, at Wray: pelage shorter than in winter-taken adults, upper parts less overlaid with black, grayer.

A young subadult taken in May three miles north of Fowler: total length 246 mm, tail 98 mm, hind foot 35 mm; weight 93 grams; postjuvenal molt beginning on sides but still concealed by soft juvenal pelage; upper parts grayer than in adults, near Pelican (47 A 2); head and shoulders lightly washed with buff; ears dark gray with light fringe; tail faintly bicolor, covered with extremely short fine hairs.

Comparisons.—*Neotoma floridana campestris* differs from all other subspecies of the Florida wood rat in lighter, more yellowish coloration.

Remarks.—Color and cranial characters show no geographic variation throughout the range of the subspecies in Colorado. Specimens of similar age and season are almost indistinguishable. Skulls vary individually in zygomatic breadth and configuration of temporal and parietal ridges.

Two skulls out of 57 examined have the interparietal divided into two elements by a distinct suture in the median line. These specimens are KU 34747 and KU 37089 from one mile south of

Wray, Yuma County. This anomaly also occurs in *N. mexicana inopinata* (see p. 287).

The range of the Florida wood rat probably extends up the Arkansas Valley nearly as far as Canon City. The westernmost locality (*15*) recorded on the map (Fig. 5) is 6 miles north and 12 miles west of Pueblo, elevation 5150 feet, where I examined a large house in a bush of *Atriplex canescens* by Turkey Creek. No rat was found, but the house was typical of those occupied by *N. floridana campestris* and unlike any den of *N. mexicana fallax*, the only other species likely to occur in that area. Localities *17*, *19*, and *20* in the lower Arkansas Valley are based on published reports unsupported by specimens but probably correctly attributed to *Neotoma floridana* (see below under additional records).

A single skull only (USNM 6301), adult male, obtained by Dr. E. Palmer, is labeled "Denver City," no collecting date. It was catalogued on 6 April 1865. The skull is undoubtedly of *N. floridana* but the locality seems questionable. Denver is considerably northwest of the nearest known locality of *floridana* today and separated by rolling open plains almost devoid of rock outcrops or other suitable shelter for this species. Dr. Palmer was primarily a plant collector whose data was usually detailed and accurate. It is possible that in his time the Florida wood rat did range northwest as far as Denver. In view of the incompleteness of this specimen and its data, however, it seems more likely that the specimen came from some locality on the plains east of Denver.

Specimens examined.—Total 54, from Colorado as follows: (*1*) Wray, Wolf's Ranch, on Olive Creek, 3500 ft., 10 (6 ERW, 2 MVZ, 2 AMNH); (*1*) Wray, 6 (2 AMNH, 1 DMNH, 1 UCM, 1 USNM, 1 BSC); (*1*) 1 mi. S Wray, 3550 and 3600 ft., 3; (*2*) Dry Willow Creek, Boyce Ranch [39° 53′ N, 102° 11′ W], 1 (DMNH); (*3*) Tuttle, 2 (BSC); (*5*) 8 mi. NE Agate, 1 (DMNH); (*6*) Cedar Point, 6 mi. NW Limon, 1 (ERW); (*8*) Olney, 12 (BSC); (*9*) 3 mi. N Fowler, 4400 ft., 7; (*10*) 1½ mi. SW Fountain, 5700 ft., 2; (*10*) 2½ mi. SW Fountain, 5700 ft., 1; (*10*) 2 mi. W and 3 mi. S Fountain, 5600 ft., 1; (*11*) 7 mi. SSE Colorado Springs, 5900 ft., 1 (MVZ); (*12*) 10 mi. S Colorado Springs, 3 (ClMNH); (*16*) Pueblo, 1 (ERW); (*18*) Fort Lyon, 1 (AMNH); (*locality in doubt*) Denver City, 1 (USNM).

Additional records.—(*4*) near Flagler, South Fork of Republican River (Cary, 1911: 114); (*7*) near Hugo, along Big Sandy (Cary, 1911: 115); (*13*) N of Piñon (Warren, 1942: 209); (*14*) Chico Basin, some 20 mi. N. Pueblo (Warren, 1942: 209); (*15*) 6 mi. N and 12 mi. W Pueblo, 5150 ft. (see above, this page); (*17*) 10 mi. N Arlington (Cary, 1911: 114); (*19*) along Arkansas River S of Chivington (Cary, 1911: 114); (*20*) near Holly, Arkansas River bottom (Warren, 1910: 112).

Neotoma lepida Thomas

Desert wood rat

Neotoma lepida Thomas, Ann. and Mag. Nat. Hist., ser. 6, 12: 235, September 1893.

Distribution.—Arid and semiarid parts of the southwestern states and extending throughout Baja California; in southern California east of the Coast Ranges and Sierra, north through Nevada into southern Oregon and Idaho, and east into northwestern Arizona and through most of Utah west of the Colorado, outside of the Wasatch and Uinta Mountains and the High Plateaus. In Colorado, only one subspecies is represented, extending into northwestern Colorado in the valleys of the Colorado and White rivers.

Diagnosis.—Size small to medium (total length 250 to 375 mm); ears proportionally large (27 to 32 mm from notch). Pelage: usually long and soft; tail short-haired and bicolored; underparts with fur basally gray and distally white or light-colored, except for a small median area of throat and breast where fur white to base. Skull: small (basilar length 30 to 40 mm) and delicate; rostrum slender; temporal ridges weak and widely separated; palatal bridge narrow, bearing a prominent median anterior spine formed by maxillaries projecting forward between incisive foramina; interpterygoid fossa narrow and sharply bounded laterally by angular rims on palatines; sphenopalatine vacuities present; incisors slender; anterointernal fold of M1 shallow or absent.

Comparisons.—*Neotoma lepida* differs from all other species of *Neotoma* known from Colorado in smaller size, shorter hind foot, and thicker more blunt anterior palatal spine. It differs from *N. cinerea* in having the tail short-haired, not bushy, and the sole of hind foot partly bare from heel to proximal plantar tubercle. The skull approaches that of *cinerea* in the channeling and shape of the interorbital region and the shape of the interpterygoid fossa; but it differs in much smaller size, shorter rostrum, more widely separated temporal ridges, and shallower anterointernal fold of M1. From *N. albigula, N. l. sanrafaeli* differs in having a smaller ventral area of fur white to base, pelage longer and softer, incisors much smaller, and posterior margin of palatal bridge usually convex. From *N. mexicana, N. l. sanrafaeli* differs in having a small but distinct area of ventral fur pure white basally, shallower anterointernal fold of M1, and narrower interpterygoid fossa. In addition to wide geographic separation across the continental divide from *N. floridana* and *N. micropus, N. l. sanrafaeli* differs from both of these in the much greater extent of basal gray coloration of ventral fur, the much narrower frontal region and interpterygoid fossa, and the notched septum. *Neotoma lepida sanrafaeli* closely resembles *Neotoma stephensi* in size and general characters but differs in having a shorter-haired, distinctly bicolor tail. *N. stephensi* occurs in Arizona and New Mexico south of the San Juan River but has not been recorded from Colorado.

Neotoma lepida sanrafaeli Kelson

Neotoma lepida sanrafaeli Kelson, Jour. Washington Acad. Sci., 39: 418, 15 December 1949.

Neotoma desertorum, Cary, Proc. Biol. Soc. Washington, 20: 25, 27 March 1907; Goldman, N. Amer. Fauna, 31: 76, 19 October 1910; Warren, The mammals of Colorado, G. P. Putnam's Sons, New York, p. 115, 1910; Cary, N. Amer. Fauna, 33: 118, 17 August 1911.

Neotoma lepida lepida, Goldman, Jour. Mamm., 13: 61, 9 February 1932; Warren, The mammals of Colorado, Univ. Oklahoma Press, Norman, p. 216, 1942.

Type.—Univ. Utah Mus. Zool. no. 6428, adult male, skin and skull; from Rock Canyon Corral, five miles southeast of Valley City, 4500 feet, Grand County, Utah; collected 20 June 1948 by Keith R. Kelson.

Range.—Outside of Colorado, this subspecies is known only from eastern Utah between the Colorado River and the High Plateaus, north to Vernal. In Colorado, it occurs in the Grand Valley north of the Colorado River and east to Palisade, and in the White River Valley near Rangely and south of Rangely approximately 20 miles along Douglas Creek. (See map, Fig. 5.)

Diagnosis.—Size small; tail short; hind feet short; ground color of upper parts generally buffy; skull ridged and channeled in the interorbital region; upper molar tooth-row long and wide.

Description.—Adults in fresh pelage taken in November, one mile southwest of Mack: size small; tail 72 per cent of head and body; hind feet short for the species; ears large (see table of measurements). Pelage: long and soft; tail short-haired; longest vibrissae 71 mm. Color: upper parts near Leghorn, 10 E 3, to Maize, 10 G 5, (R: near Light Buff, XV 17′ e, to near Warm Buff, XV 16′ d), heavily streaked with black guard hairs; sides lighter and brighter (Peach Blow, 10 B 5; R: near Capuchin Buff), thinly streaked with black guard hairs; brightest on shoulders and cheeks; ears dark gray; underparts white, fur gray basally except in small areas 10 to 25 mm wide on pectoral and inguinal regions where white to base; slightly orange-buffy pectoral band present in some specimens, not extending to midventral line; tail bicolor, medium to dark gray above, whitish below with dull buffy basal band; feet white.

Skull: small and light, rostrum slender, somewhat arched in frontonasal region; zygomatic arches narrow and delicate; braincase smoothly rounded; nasals narrowed posteriorly; dorsal extensions of premaxillaries narrow and extending far posterior to nasals; frontals moderately channeled between angular supraorbital ridges; temporal ridges moderate, widely flaring; interparietal roughly rectangular or pentagonal, its length equal to about half its width; incisive foramina spindle-shaped; palatal bridge relatively long and narrow; anterior palatal spine stout, blunt; vomer separated from anterior palatal spine by notch in septum; posterior edge of palatal bridge convex and usually slightly bilobed; interpterygoid fossa narrow, sharply bounded laterally by straight, slightly diverging, angular rims on palatines; sphenopalatine vacuities long and moderately wide; bullae moderate, not greatly inflated; incisors slender; upper molar tooth-row long and wide (both relatively and absolutely); anterointernal fold of M1 faint or absent.

Adults in somewhat worn pelage taken in April one mile southwest of Mack: upper parts less streaked with blackish, having rather a more brownish-gray wash than adults in fresh pelage.

Two immature specimens taken in April, one mile southwest of Mack: total length 200 and 198 mm, length of tail 80 and 78 mm, respectively; full juvenal pelage soft and fine; upper parts lighter than in adults and grayish, not so buffy; tail only slightly bicolor, sparsely haired with extremely short hairs.

Comparisons.—*N. l. sanrafaeli* does not differ significantly in color from *N. l. lepida*. The skull of *sanrafaeli* is more ridged and channeled above and has a somewhat longer palatal bridge and upper molar tooth-row. In other cranial measurements taken, the subspecies does not differ from *lepida* (Goldman, 1910: 76). From *N. l. monstrabilis*, *sanrafaeli* differs as follows: color lighter than in most *monstrabilis*, especially the under parts, which lack the buffy wash on the belly and the pectoral band; skull more ridged and channeled above; upper molar tooth-row and palatal bridge averaging slightly longer.

Remarks.—Goldman (1910: 78), Warren (1910: 115), and Cary (1911: 118) referred specimens from five miles west of Rangely to *Neotoma desertorum*, which at that time was considered to include the desert wood rats ranging from southeastern California through most of Nevada, Utah and Arizona north and west of the Colorado River. In 1932 Goldman revised the wood rats of the *Neotoma Lepida* group, recognizing the name, *Neotoma l. lepida* in place of *Neotoma desertorum*. At the same time, he described as a new subspecies, *Neotoma lepida monstrabilis*, those specimens from southern Utah and northwestern Arizona west of the Colorado River. In eastern Utah and Colorado, there was left of *N. l. lepida*, only the four specimens from near Rangely. These were not mentioned by Goldman, except by implication in his account of the distribution of *N. l. lepida* (Goldman, 1932: 62), which includes as well, however, the range ascribed (*loc. cit.*) to *N. l. monstrabilis*. Warren (1942: 216) referred the specimens from Rangely, Colorado, to *N. l. lepida*. Subsequently, additional specimens of *N. lepida* were collected from eastern Utah between the Colorado River and the High Plateaus. Kelson (1949: 418) described these Utah specimens as a new subspecies, *Neotoma lepida sanrafaeli*, and questioned on distributional grounds the designation of the Rangely, Colorado, specimens as *N. l. lepida*. Durrant (1952: 342)

continued on p. 332

TABLE 1.—MEASUREMENTS OF ADULT WOOD RATS

Mean and extremes or catalog number	Number averaged and sex	Total length	Length of tail	Length of hind foot	Length of ear	Weight	Basilar length	Length of nasals	Zygomatic breadth	Interorbital breadth	Breadth of rostrum	Diastema	Alveolar length of maxillary tooth-row	Length of incisive foramina	Length of palatal bridge
		N. cinerea orolestes, Gunnison County, Colorado													
Mean	10	389	164	43	32^{3}	341^{3}	42.2	19.8^{9}	25.8	5.9	7.5	14.4	10.1	11.5	9.1
Min.	♂	353	146	40	31	231	39.5	18.9	24.3	5.4	7.1	13.4	9.5	9.9	8.3
Max.	......	420	176	46	34	410	46.6	20.7	28.1	6.5	7.8	16.0	10.7	12.3	10.0
Mean	6	374	161	42	31	296	41.5	19.8	26.0	5.8	7.4	14.5	9.8	11.4	8.9
Min.	♀	353	156	40	30	280	40.3	17.9	25.0	5.7	7.0	14.1	9.5	10.6	8.3
Max.	......	386	166	43	32	315	42.6	20.9	27.3	6.2	7.7	14.9	10.4	12.2	9.6
		Boulder County, Colorado													
Mean	11	390^{5}	170^{5}	43^{5}	32^{1}	259^{1}	42.2^{10}	19.5	25.6^{10}	5.7	7.5	14.6	10.0	11.2	9.1
Min.	♂	366	155	40	......	......	38.5	17.1	24.3	5.4	6.8	12.7	9.3	9.9	7.9
Max.	......	419	188	45	......	......	44.8	21.3	27.7	6.2	8.0	16.7	10.5	12.4	10.0
Mean	7	340^{6}	151^{6}	40^{6}	31^{2}	296^{2}	40.0^{4}	18.5	20.8^{6}	5.9	7.3	14.2	9.5	10.8	8.8
Min.	♀	273	144	38	30	281	37.6	17.4	23.6	5.4	6.8	13.8	9.2	10.1	8.3
Max.	......	373	159	42	32	312	42.4	19.2	26.4	6.2	7.7	14.9	10.0	11.1	9.4

		N. c. arizonae, northeastern Arizona													
Mean	4	385^3	158^3	40	......	......	42.0	19.6^2	25.5	5.7	7.4	14.3	9.4	11.2	8.6
Min.	♂	365	153	38	......	......	40.2	19.3	24.7	5.4	7.1	13.9	8.8	10.7	8.0
Max.		398	168	42	......	......	43.7	20.0	26.3	5.9	7.6	14.8	9.7	12.0	9.2
Mean	7	330^5	146^5	36^5	......	......	37.8	17.9	23.7	5.4	7.1	13.1	9.0	10.5	8.0
Min.	♀	302	127	32	......	......	36.4	16.6	22.7	5.2	6.8	12.4	8.6	9.9	7.6
Max.		358	165	40	......	......	39.2	18.9	24.7	5.7	7.5	14.0	9.9	11.3	8.5
		Montezuma County, Colorado													
Mean	5	351	152	39	34^2	243^2	39.2	18.7	21.4	5.5	7.3	13.5	9.2	11.0	8.4
Min.	♂	330	148	33	33	233	37.0	17.1	23.2	5.2	7.0	12.8	8.7	9.4	7.8
Max.		368	156	43	35	253	41.8	19.2	25.2	6.1	7.5	14.8	9.8	11.8	9.5
Mean	8	343	151	39	29^1	152^1	39.4	18.5	24.3	5.6	7.3	13.3	9.3	10.9	8.2
Min.	♀	319	137	34	......	......	36.1	16.7	22.0	5.2	6.8	11.9	8.7	10.0	7.8
Max.		381	168	43	......	......	42.3	20.6	26.0	6.1	7.8	14.5	10.1	11.8	8.5
		Moffat County, Colorado													
Mean	8	353^6	154^6	40	36^4	209^1	40.0	18.7	24.6	5.7	7.2	13.8	9.3	10.9	8.7
Min.	♂	336	143	35	33	......	37.5	17.5	23.0	5.2	6.7	12.4	8.9	9.4	8.2
Max.		384	166	44	38	......	42.5	20.7	26.2	6.2	7.9	15.8	9.8	11.7	9.5
Mean	6	345	147	40	33^2	......	38.7	18.2^5	24.0	5.7	7.2	13.2	9.5	10.4	8.4
Min.	♀	309	141	38	32	......	36.4	17.0	22.2	5.4	6.7	12.4	9.2	9.7	7.6
Max.		365	157	44	34	......	41.4	18.7	26.1	5.9	7.7	14.5	9.9	11.6	9.1

TABLE 1.—*Continued*

Mean and extremes or catalog number	Number averaged and sex	Total length	Length of tail	Length of hind foot	Length of ear	Weight	Basilar length	Length of nasals	Zygomatic breadth	Interorbital breadth	Breadth of rostrum	Diastema	Alveolar length of maxillary tooth-row	Length of incisive foramina	Length of palatal bridge
		N. c. arizonae, Kinney Ranch and Antelope Ranch, Wyoming													
Mean........	11	364	156	42	36^{4}	272^{1}	41.0	19.3^{10}	25.4	5.8	7.4	14.2	9.6	11.1	9.1
Min..........	♂	341	137	40	34	......	37.1	17.4	22.6	5.3	6.9	12.4	9.1	10.1	8.7
Max..........	......	399	173	45	40	......	42.5	21.0	26.2	6.0	7.9	15.0	10.2	11.9	9.6
Mean........	5	344	149	39	34^{1}	178^{1}	38.5	18.0^{4}	24.3	5.9	7.1	12.9	9.7	10.6	8.3
Min..........	♀	336	144	37	......	......	36.3	17.2	22.1	5.4	6.4	11.8	9.3	9.9	8.1
Max..........	......	351	153	41	......	......	40.0	19.3	25.9	6.4	7.5	13.6	10.2	11.3	8.8
		N. c. rupicola, 1 mi. N Geary's Reservoir, Colorado													
Mean........	4	366	160	41	......	......	40.9^{3}	20.6	24.8^{3}	5.9^{3}	7.6	14.6	9.9	11.8	8.5
Min..........	♂	342	158	40	......	......	37.9	19.3	24.0	5.4	7.1	13.6	9.6	10.9	8.1
Max..........	......	385	164	42	......	......	42.9	21.6	25.2	6.3	7.9	15.0	10.3	12.4	8.8
Mean........	6	336	147	40	......	......	39.6	19.0	25.0	5.6	7.5	13.7	9.9	11.5	8.2
Min..........	♀	314	140	38	......	......	37.5	18.3	23.0	5.4	6.7	12.7	9.6	10.4	7.9
Max..........	......	361	158	41	......	......	41.5	20.2	26.3	6.1	8.6	14.8	10.1	12.6	8.7

		N. c. rupicola, 21 mi. N and 5 mi. E Stoneham, Colorado													
37146	♂	337	142	42	32	240	38.6	18.9	24.8	6.1	7.2	13.1	9.6	10.5	8.7
37147	♂	362	153	44	32	280	41.3	20.0	25.1	5.8	7.2	14.0	10.3	11.6	8.5
37145	♀	369	156	44	33	320	41.5	20.6	25.8	5.7	7.6	14.5	10.8	11.3	9.0
		N. mexicana fallax, Loveland, Colorado													
Mean	8	346[6]	155[6]	34	......	......	36.8	17.7	23.5	5.4	6.9	12.4	9.2	9.6	8.3
Min.	♂	325	144	33	......	......	35.4	16.3	22.3	5.2	6.6	11.4	8.8	8.9	7.8
Max.	......	361	167	34	......	......	38.5	18.8	24.6	5.6	7.1	13.3	9.5	10.2	8.7
Mean	8	321	141	32	......	......	35.1	16.6	22.6	5.3	6.8	11.9	9.1	9.0	8.1
Min.	♀	303	132	30	......	......	33.8	15.9	21.8	5.1	6.5	11.3	8.7	8.5	7.9
Max.	......	334	150	34	......	......	36.9	17.6	23.5	5.5	7.0	12.9	9.4	9.8	8.6
		El Paso County, Colorado													
Mean	8	333	143	35	26[3]	......	36.8	18.1[7]	22.8	5.5	7.0	12.6	9.3	9.6	8.4
Min.	♂	314	132	33	25	......	35.3	17.1	21.7	5.2	6.5	11.8	9.0	8.9	7.7
Max.	......	351	154	38	28	......	38.0	19.5	23.9	5.7	7.3	13.7	9.7	10.0	9.3
Mean	6	327	148	33	25[5]	......	36.2	18.1	23.3	5.2	7.0	12.4	9.2	9.4	8.2
Min.	♀	307	140	31	23	......	35.0	17.1	22.8	4.9	6.9	11.9	8.8	9.0	7.8
Max.	......	350	154	35	26	......	37.3	18.8	23.6	5.6	7.3	12.7	9.8	9.6	8.9

TABLE 1.—*Continued*

Mean and extremes or catalog number	Number averaged and sex	Total length	Length of tail	Length of hind foot	Length of ear	Weight	Basilar length	Length of nasals	Zygomatic breadth	Interorbital breadth	Breadth of rostrum	Diastema	Alveolar length of maxillary tooth-row	Length of incisive foramina	Length of palatal bridge
		N. m. scopulorum, vicinity of Two Buttes, Colorado													
Mean........	4	359	148	36	26[2]	246[2]	38.1	19.3	24.0	5.2	7.2	12.9	9.5	9.8	8.8
Min..........	♂	345	140	32	26	238	37.1	18.5	23.4	4.9	6.9	12.5	9.3	9.2	8.4
Max..........	......	368	158	38	26	253	38.9	20.0	24.5	5.5	7.7	13.3	9.8	10.2	9.2
DM4311......	♀	310	138	35	......	......	35.8	17.9	23.9	5.1	6.9	11.8	9.7	8.6	8.6
37139........	♀	379	178	38	26	246	37.7	19.6	23.7	5.0	6.7	12.7	9.7	9.9	8.5
37141........	♀	369	169	37	25	231	38.6	18.1	24.0	5.3	6.9	13.7	9.2	10.2	8.9
		Trinidad, Colorado													
$\frac{\text{BSC35223}}{47488}$....	♂	330	147	31	......	......	35.9	17.4	23.5	5.4	7.1	12.2	9.2	9.6	8.1
$\frac{\text{BSC35222}}{47487}$....	♂	360	164	32	......	......	36.5	17.7	24.9	5.4	6.7	13.2	8.5	9.7	8.6
$\frac{\text{BSC35221}}{47486}$....	♂	335	145	32	......	......	37.2	18.5	24.0	5.2	7.1	12.7	8.9	9.8	8.6

N. m. scopulorum, 3 mi. W San Acacio, Colorado														
Mean	5	318	128	34	27	......	36.1	18.4	23.1	5.4	7.2	12.3	9.3	9.0	8.5
Min.	♂	297	115	32	25	......	35.6	17.6	22.0	5.2	6.8	12.0	9.0	8.2	7.9
Max.	......	333	142	36	28	......	36.7	19.3	23.9	5.6	7.6	12.9	9.8	9.4	9.0
Mean	6	311	132	34	27	......	35.6	18.0	22.1	5.3	6.8	12.2	9.1	9.0	8.5
Min.	♀	300	125	32	25	......	34.5	17.5	21.5	5.0	6.4	11.6	8.4	7.6	8.2
Max.	......	321	136	35	29	......	36.9	19.0	22.7	5.8	7.1	13.0	9.7	9.6	8.8
N. m. inopinata, Montezuma County, Colorado														
Mean	6	322^5	144^5	34	27^1	......	34.1	17.1	22.0	5.0	6.4	11.4	9.0	9.0	7.9
Min.	♂	314	141	33	......	......	33.3	16.3	21.6	4.6	6.0	11.1	8.7	8.9	7.3
Max.	......	328	147	36	......	......	35.4	18.2	22.4	5.4	6.5	11.6	9.7	9.3	7.9
La Plata County, Colorado														
Mean	5	328	148	35	27	168	34.7	17.7	22.1	5.3	6.6	11.9	8.9	9.1	8.1
Min.	♀	322	144	34	26	151	33.8	17.1	21.3	5.1	6.1	11.7	8.6	8.6	7.9
Max.	......	336	151	36	29	191	25.7	18.5	23.0	5.6	7.3	12.5	9.1	9.4	8.3
Mesa County, Colorado														
Mean	4	313^3	139^3	34	26^3	......	33.8	16.9	21.5	5.2	6.3	11.2	9.1	8.7	7.7
Min.	♂	306	132	34	25	......	32.9	16.4	21.0	4.9	6.1	10.7	9.0	8.4	7.5
Max.	......	317	144	35	28	......	34.9	17.7	22.1	5.3	6.5	11.7	9.3	8.9	8.1
ERW4087	♀	305	140	33	28	......	33.0	16.4	20.5	4.9	5.9	11.1	8.5	8.8	7.6
ERW995	♀	309	142	32	......	......	33.2	16.6	20.6	5.1	6.4	10.5	9.1	8.8	8.0
ERW4086	♀	310	137	33	28	......	34.7	17.4	20.9	5.2	6.2	11.8	8.6	8.8	8.0

TABLE 1.—*Continued*

Mean and extremes or catalog number	Number averaged and sex	Total length	Length of tail	Length of hind foot	Length of ear	Weight	Basilar length	Length of nasals	Zygomatic breadth	Interorbital breadth	Breadth of rostrum	Diastema	Alveolar length of maxillary tooth-row	Length of incisive foramina	Length of palatal bridge
		N. albigula brevicauda, Mesa County, Colorado													
34749........	♂	......	......	34	30	200	37.7	17.5	23.1	5.9	7.5	12.4	8.6	9.5	7.6
Mean........	4	324	142	34	28	160	35.4	16.7	22.6	5.7	7.2	11.8	8.4	9.5	7.0
Min..........	♀	307	131	33	28	146	33.7	16.0	22.2	5.6	6.9	10.9	7.9	8.9	6.9
Max..........	......	339	150	35	29	169	36.5	17.2	23.4	5.9	7.5	12.5	8.9	9.7	7.2
		Montrose County, Colorado													
Mean........	4	302	130	34	......	......	35.2	15.5	22.0	5.8	7.0	11.7	7.8	8.8	7.0
Min..........	♀	285	120	32	......	......	33.8	14.7	21.0	5.8	6.4	10.8	7.4	7.9	6.3
Max..........	......	322	140	35	......	......	36.5	16.0	23.4	5.9	7.4	12.5	8.3	9.5	7.3

N. a. laplataensis, La Plata County, Colorado															
34763........	♂	294	120	34	25	151	32.7	....	21.8	5.7	6.8	10.2	7.9	7.8	7.0
DMNH721....	♂	290	128	31	......	......	33.9	14.6	21.7	5.5	6.9	11.1	8.3	8.1	6.9
Mean........	5	308	137	34	29	151	34.6	16.0	21.7	5.7	6.7^4	11.3	8.4	8.8	7.2
Min..........	♀	288	132	32	28	123	32.8	15.5	20.4	5.5	6.5	10.3	7.9	8.2	6.9
Max..........	......	333	143	36	30	181	36.1	16.6	22.8	5.8	7.2	12.2	8.9	9.4	7.4
N. a. warreni, Gaume's Ranch, Colorado															
Mean........	4	316	131	36	......	......	36.8	16.6	23.5	5.5	7.0	12.2	8.8	8.8	7.8
Min..........	♂	304	120	34	......	......	36.1	15.8	22.6	5.1	6.8	11.8	8.6	8.6	6.9
Max..........	......	326	143	36	......	......	37.5	17.4	24.8	5.9	7.1	12.4	9.0	9.0	8.4
Mean........	7	320	141	35	......	......	35.6^5	16.6^5	23.2^6	5.8	7.1	11.9^6	8.6	9.0^6	7.7
Min..........	♀	304	125	34	......	......	35.0	16.1	22.5	5.5	6.8	11.4	8.2	8.5	7.4
Max..........	......	332	152	37	......	......	36.3	17.3	23.8	6.0	7.4	12.6	9.0	9.9	8.1
Otero County, Colorado															
Mean........	4	338	140	36	28^3	224^3	38.5	17.4	23.8	5.8	7.2	13.3	8.5	9.3	7.6
Min..........	♂	320	126	36	27	200	37.3	17.0	23.2	5.7	7.1	12.8	7.7	8.4	7.2
Max..........	......	354	147	37	28	243	39.1	17.7	24.7	5.9	7.3	13.8	9.0	9.9	8.0
Mean........	5	324	139	36	27	177	37.0	17.1	23.1	5.4	7.0	12.6	8.4	9.2	7.6
Min..........	♀	308	128	35	25	148	35.6	16.4	22.5	5.2	6.6	12.0	7.8	8.9	7.3
Max..........	......	332	147	37	28	213	38.7	18.1	23.7	5.6	7.6	13.4	8.8	9.5	7.8

TABLE 1.—*Concluded*

Mean and extremes or catalog number	Number averaged and sex	Total length	Length of tail	Length of hind foot	Length of ear	Weight	Basilar length	Length of nasals	Zygomatic breadth	Interorbital breadth	Breadth of rostrum	Diastema	Alveolar length of maxillary tooth-row	Length of incisive foramina	Length of palatal bridge
		N. a. warreni, 2 mi. E Wetmore, Colorado													
37102	♀	345	154	37	29	245	39.5	18.2	25.8	5.7	7.3	13.5	8.9	9.5	7.9
		N. micropus canescens, Baca County, Colorado													
Mean	4	349	142	39	25[1]	236[1]	40.1	19.2	27.1	6.3	8.1	13.8	9.4	10.8	8.1
Min.	♂	338	137	36	......	......	38.3	18.2	25.2	5.8	7.6	13.2	8.9	10.1	7.7
Max.		361	149	42	......	......	41.6	20.5	28.1	6.5	8.5	14.4	9.7	11.1	8.7
Mean	5	339	138	37	26[2]	243[2]	39.2	18.9	26.3	6.1	7.7	13.6	9.0	10.6	8.0
Min.	♀	325	128	36	25	241	37.7	17.6	24.7	5.7	7.1	12.4	8.3	9.6	7.3
Max.		353	147	39	27	246	41.4	20.5	27.9	6.6	8.3	15.0	9.7	11.7	9.0

N. floridana campestris, Yuma County, Colorado															
Mean	8	351	140	41	......	......	39.2	18.7	25.7	6.8	8.0	12.9	9.6	9.8	8.2
Min.	♂	304	118	40	......	......	35.0	16.7	23.8	6.3	7.6	10.7	8.7	8.9	7.6
Max.	......	389	167	44	......	......	43.0	20.6	27.8	7.6	8.5	15.1	10.1	10.7	9.0
Mean	9	351	145	41	26^{2}	254^{2}	38.8^{8}	18.5	25.2^{8}	6.6	7.9	12.8	9.7	9.7	8.0
Min.	♀	308	121	38	25	253	35.0	16.4	23.0	6.3	7.3	10.8	9.3	8.8	7.4
Max.	......	389	168	43	27	255	40.8	19.3	26.4	7.0	8.2	13.9	10.3	10.7	8.7
Crowley County, Colorado															
Mean	7	350	146	40	......	......	39.4^{6}	18.2^{6}	26.1^{6}	6.5	7.9^{6}	12.9^{6}	9.4	10.0	7.6
Min.	♂	320	118	36	......	......	38.2	17.6	25.6	6.2	7.7	12.4	9.2	9.4	7.4
Max.	......	380	162	43	......	......	40.7	18.6	26.7	7.1	8.2	13.4	9.8	10.3	7.9
Mean	8	346	147	39	26^{3}	282^{3}	39.2	18.1	25.8	6.4	7.8	13.0	9.3	10.0	7.6
Min.	♀	325	131	38	25	241	37.3	17.2	24.7	6.1	7.5	12.2	9.1	9.6	7.3
Max.	......	365	157	40	28	342	40.6	18.7	26.9	6.9	8.1	13.8	9.6	10.5	8.4
N. lepida sanrafaeli, Mesa County, Colorado															
Mean	5	283	116	32	30^{4}	122^{3}	32.7	14.8	20.5	5.2	6.0	10.2	8.4	8.2	7.3
Min.	♂	263	103	31	29	108	31.5	14.3	19.5	5.0	5.9	9.5	8.2	7.6	7.0
Max.	......	294	126	33	30	136	35.1	15.5	22.0	5.3	6.2	11.1	8.7	8.6	7.6
Mean	6	275	114	32	30	107^{4}	31.1^{5}	14.2	19.7	5.0	5.8	9.8	8.2	8.0	7.0
Min.	♀	266	110	31	28	104	30.0	13.6	18.9	5.0	5.6	9.2	7.9	7.6	6.8
Max.	......	287	122	32	31	111	32.0	14.8	20.3	5.1	6.1	10.6	8.4	8.6	7.2

Superscript numerals indicate the number actually averaged.

expressed the suspicion that the specimens from Colorado either are referable to *N. l. sanrafaeli* or represent an unnamed kind.

Neotoma l. sanrafaeli is a weakly marked geographic race fairly constant in color but more variable in skull characters. Specimens of the desert wood rat examined from northwestern Colorado are indistinguishable from those from eastern Utah and are here referred to the same subspecies.

On the basis of known records of occurrence of *sanrafaeli,* I expect that it can be found on the north side of the White River and east up the White River Valley possibly almost to Meeker. In the Grand Valley it may occur on the north side of the Colorado River as far east as Grand Valley or even Rifle. In Moffat County, ranchers near Pat's Hole at the junction of the Yampa and Ladore canyons mentioned a "file-tailed rat" found on the flank of the Yampa Plateau south of Yampa Canyon. The animal referred to may be *Neotoma lepida,* which may be expected to occur in that area.

Specimens examined.—Total 21, from Colorado as follows: (*1*) 5 mi. W Rangely, 5300 ft., 4 (BSC); (*2*) 2 mi. E and 18 mi. S Rangely, 6200 ft., 2; (*2*) Douglas Creek, 19 mi. S Rangely, 1 (CM); (*3*) 1 mi. SW Mack, 4540 and 4600 ft., 12 (6 ERW); (*4*) 1½ mi. S Loma, 4600 ft., 2.

Additional record.—(*5*) foot of Book Cliffs, 5 mi. W Palisade, 1 (Sutton, *in litt.*).

ECOLOGY

The scope of the study reported in the following sections has been limited by emphasis on those aspects of ecology thought to have most direct influence on the distribution of wood rats. Other aspects of ecology have been studied only secondarily, and as favorable opportunities presented themselves. Hence the following accounts do not give a complete or balanced picture of the life history of any species. Greatest attention has been given to the habitats, shelter, and food habits of the six species in Colorado. Most of the information was obtained by the analysis of dens at which wood rats were obtained. Den-analysis forms were prepared on field note paper in order to assure the recording of significant facts of the den study, and in order to facilitate the comparison of all den records. Other noteworthy observations which could not be recorded on the form sheets were described separately in the field notebook. Important plants and animals that could not be positively identified in the field were collected for later museum study. Photographs were taken of nearly every wood rat den and habitat where specimens were collected.

In all, 176 dens from 70 localities were examined in some detail. The number of dens studied for each species follows:

N. cinerea	57	*N. floridana*	12
N. mexicana	51	*N. lepida*	9
N. albigula	39		
N. micropus	8	Total	176

The localities at which these dens were studied are shown on the map, Fig. 1. The greatest number of species found living at any one locality was three.

The months in which field work was done are shown below for each species:

N. cinerea: May, June, July, Aug., Sept., Oct., Nov.; *N. mexicana*: May, June, July, Aug., Sept., Oct., Nov.; *N. albigula*: May, June, Aug., Sept., Oct., Nov.; *N. micropus*: May, June; *N. floridana*: May, June, Nov.; *N. lepida*: Sept., Nov.

Information on the bushy-tailed wood rat was obtained also in the summers of 1948 and 1949 by live-trapping and marking individuals of a small population three miles north of Almont. Live rats were weighed, marked by toe-clipping, and examined for parasites, reproductive condition, and condition of pelage. Some individuals were dyed with Roux oil shampoo tint as an aid in identifying pelages and molts upon recapture at a later date. Behavior of wild rats was observed in daylight by release of live-trapped individuals and at night by watching at occupied dens with the aid of visual red spotlights.

Habitat

It is convenient to describe the habitat of an individual wood rat or of a local population in terms of the life-zone, plant community, topography, and substrate, but these terms alone do not suffice to describe the habitat adequately. An individual wood rat sometimes forages over two or more very different plant communities or types of topography. Frequently the dens are in ecotones, or in marginal situations with respect to topography or substrate. The limits of distribution of wood rats seem rarely to coincide with the limits of life-zones, communities, topographic features, or types of substrate unless the limit is also a physical barrier to the rat.

Life-zones have been recorded at each den that was studied. But the mere recognition of a zone by the prevalence of indicator plants often gives a misleading impression of the habitat, because many dens were in areas where the life-zones were not at all in typical expression. The biotic community directly touching the life of the individual wood rat is composed principally of those plants growing in a very limited area around the den, and these plants often do not represent the principal association prevailing in the general area. Frequently the den is situated at the margin of two communities, or in a seral stage, or in a narrow belt of distinctively different local character. These situations are usually controlled by the character of the topography and substrate. For these reasons the formal names of the principal biotic associations have not been recorded. Instead the local community prevailing within about 50 yards of each den has been designated by a common descriptive name or by the two or three dominant plants of the community, without regard to its rank or relation to the climax.

Shelter

The physical aspect of the environment seems to have greater importance for the survival of wood rats than the kinds of plants present, because of the necessity for suitable shelter, and its relative scarcity. The available food supply, in comparison, is generally abundant and varied.

Wood rats make their dens either in ready-made kinds of shelter, such as rock crevices or abandoned buildings, or in houses which they construct for themselves of sticks, cactus or other material. The ability both to utilize natural shelters and to build dens where none is available enables them to occupy a great variety of habitats and situations and maintain themselves against innumerable enemies and adverse conditions. Not every kind of wood rat makes use of every type of shelter, however. Hence the ability of each kind of rat to exploit naturally available shelter and to make use of local building materials is an important factor accounting for some of the differences in the distribution of wood rats.

Previous reports on the natural history of wood rats have not been in agreement on the use of terms for different kinds of shelter. The word "nest," particularly, has sometimes been used loosely, with the possibility of confusion. In this report such terms will be used with the following meanings: *den,* any large outer shelter enclosing one or more chambers or passages used by the occupant as living spaces; *house,* a kind of den constructed by its occupant, or a former occupant, out of materials gathered together to provide shelter; *nest,* a small inner resting place formed of soft fibrous material, where the occupant sleeps, rests, or cares for its newborn young.

Food

The determination of kinds of food eaten is a basic prerequisite for any comparative study of food habits, although kinds of food may not be as significant for many animals as availability, quantities, or other aspects of food habits. Since wood rats are almost entirely herbivorous, the study of food is, in this instance, almost entirely a study of plants. Insects and other animal food are eaten, probably in small amounts, but no special effort was made in this study to determine the kinds and importance of animal food eaten.

Information concerning the foods of wood rats in Colorado was obtained primarily by the examination of dens at which wood rats were trapped. The kinds of plant remains found in the food litter at each den were compared with the kinds of plants available to the rat within an estimated distance of 100 feet of the den. Of those plants that could not be definitely recognized in the field, pressed specimens were prepared and submitted to botanists for identification.

Before the accounts of food eaten by each kind of wood rat are presented, it may facilitate the comparison of the accounts to list in summary all of the 219 kinds of plants for which evidence was obtained of use by any kind of wood rat. The plants are listed by scientific name, in alphabetical order within the following major ecological groupings by life-form: trees, shrubs, cacti, vines, grasses, and forbs. Following each scientific name is the common name. Elsewhere in this report common names of plants are not followed by scientific names if the plant is included in this list. Under each kind of plant are listed the subspecies of wood rats that eat it, together with the months in which I secured evidence of its use as food. For comparison with the months in which field work was done, see page 333.

List of Plants Eaten by Wood Rats in Colorado

(with months in which evidence of use as food was obtained)

TREES

Abies lasiocarpa (Hook.) Nutt. Alpine fir
- *N. cinerea orolestes,* July, Aug.

Acer glabrum Torr. Rocky Mountain maple
- *N. cinerea orolestes,* Aug., Sept.

Alnus tenuifolia Nutt. Mountain alder
- *N. cinerea orolestes,* July, Aug.
- *N. mexicana inopinata,* Oct.

Celtis occidentalis L. Hackberry
- *N. cinerea rupicola,* June

Fraxinus anomala Torr. Singleleaf ash
- *N. mexicana inopinata,* June
- *N. lepida sanrafaeli,* Nov.

Juniperus monosperma (Engelm.) Sarg. One-seed juniper
- *N. mexicana fallax,* Sept.
- *N. mexicana scopulorum,* May
- *N. albigula warreni,* May

Juniperus scopulorum Sarg. Rocky Mountain juniper
- *N. cinerea orolestes,* July, Sept.
- *N. mexicana fallax,* Nov.
- *N. mexicana inopinata,* June, Aug., Oct., Nov.
- *N. albigula laplataensis,* Oct.
- *N. micropus canescens,* May

Juniperus utahensis (Engelm.) Lemm. Utah juniper
- *N. cinerea orolestes,* Nov.
- *N. cinerea arizonae,* Aug., Sept., Oct., Nov.
- *N. mexicana inopinata,* June, Aug., Sept., Oct., Nov.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Aug., Sept., Oct., Nov.
- *N. lepida sanrafaeli,* Sept. Nov.

Picea engelmanni Parry, Engelmann spruce
- *N. cinerea orolestes,* June, July, Aug.

Picea pungens Engelm. Blue spruce
- *N. cinerea orolestes,* July

Pinus aristata Engelm. Bristlecone pine
- *N. cinerea orolestes,* July, Aug.

Pinus edulis Engelm. Piñon
- *N. cinerea orolestes,* May, Nov.
- *N. cinerea arizonae,* Aug., Sept.
- *N. mexicana fallax,* Sept.
- *N. mexicana inopinata,* June, Aug., Oct., Nov.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Aug., Sept., Oct., Nov.
- *N. albigula warreni,* May

Pinus flexilis James. Limber pine
- *N. cinerea orolestes,* Sept.

Pinus ponderosa Dougl. Ponderosa pine
- *N. cinerea orolestes,* July, Sept.
- *N. mexicana fallax,* Aug.
- *N. mexicana inopinata,* Aug., Sept., Nov.

Populus angustifolia James. Narrowleaf cottonwood
- *N. cinerea orolestes,* Nov.

Populus sargentii Dode. Plains cottonwood
- *N. albigula warreni,* May
- *N. floridana campestris,* May

Populus tremuloides Michx. Aspen
- *N. cinerea orolestes,* June, July, Aug.

Populus wislizeni (S. Wats.) Sarg. Rio Grande cottonwood
- *N. mexicana inopinata,* Oct.

Pseudotsuga taxifolia (Poir.) Britt. Douglas-fir
- *N. cinerea orolestes,* July, Aug., Sept.
- *N. mexicana inopinata,* Aug.

SHRUBS

Amelanchier alnifolia Nutt. Western serviceberry
  N. cinerea orolestes, July, Sept.
  N. mexicana inopinata, Aug.

Amelanchier pumila Nutt.
  N. cinerea orolestes, Aug.

Amelanchier utahensis Koehne. Utah serviceberry
  N. cinerea arizonae, Aug.
  N. mexicana inopinata, June, Aug.

Amelanchier. Serviceberry
  (Records other than as reported under species of *Amelanchier*)
  N. mexicana inopinata, Sept.
  N. albigula laplataensis, Sept.

Artemisia frigida Willd. Mountain sage
  N. cinerea orolestes, July
  N. cinerea arizonae, Aug. Sept.
  N. mexicana fallax, Sept.

Artemisia pacifica Nutt.
  N. cinerea orolestes, July

Artemisia tridentata Nutt. Sagebrush
  N. cinerea orolestes, May, July, Aug., Sept.
  N. cinerea arizonae, Aug.
  N. mexicana inopinata, June, Aug., Nov.
  N. albigula brevicauda, June
  N. albigula laplataensis, June, Aug., Oct., Nov.
  N. lepida sanrafaeli, Sept., Nov.

Artemisia sp. (Shrub).
  N. albigula warreni, May

Atriplex canescens (Pursh) Nutt. Gray saltbush
  N. cinerea orolestes, Sept., Nov.
  N. cinerea arizonae, Aug., Oct.
  N. mexicana scopulorum, May
  N. mexicana inopinata, June, Aug., Nov.
  N. albigula brevicauda, June
  N. albigula laplataensis, Aug.
  N. floridana campestris, May

Atriplex confertifolia (Torr. and Frem.) Wats. Shadscale
  N. cinerea arizonae, Aug., Sept., Oct., Nov.
  N. mexicana inopinata, Sept., Nov.
  N. albigula laplataensis, Sept.
  N. floridana campestris, May
  N. lepida sanrafaeli, Sept., Nov.

Atriplex nuttallii S. Wats. Nuttall saltbush
  N. lepida sanrafaeli, Nov.

Atriplex cf. A. *nuttallii* S. Wats.
  N. cinerea arizonae, Sept.
  N. albigula laplataensis, Aug.

Brickellia californica (T. and G.) A. Gray. California brickellbush
  N. mexicana scopulorum, May
  N. mexicana inopinata, June, Aug.

Brickellia scabra, (A. Gray) A. Nels.
  N. mexicana inopinata, Aug.

Brickellia. Brickellbush
  (Records other than as reported under species of *Brickellia*)
  N. cinerea orolestes, Oct.

Ceanothus fendleri Gray. Fendler ceanothus
  N. cinerea orolestes, Sept.
  N. mexicana fallax, Nov.

Cercocarpus intricatus S. Watson. Littleleaf mountain-mahogany
  N. cinerea arizonae, Aug.

Cercocarpus montanus Raf. Mountain-mahogany
  N. cinerea orolestes, Nov.
  N. cinerea arizonae, Aug., Sept.
  N. mexicana fallax, July, Aug.
  N. mexicana inopinata, June, Aug., Sept., Oct.
  N. albigula warreni, May

Chrysothamnus greenei greenei (H. and C.) Harrington. Greene's rabbitbrush
  N. cinerea orolestes, July

Chrysothamnus nauseosus (Pallas) Britt. Rubber rabbitbrush

N. cinerea orolestes, Sept., Nov.
N. cinerea arizonae, Aug., Sept., Oct.
N. cinerea rupicola, June
N. mexicana inopinata, June, Aug., Sept., Oct.
N. albigula laplataensis, Sept., Nov.
N. floridana campestris, May

Chrysothamnus parryi (A. Gray) Greene. Parry rabbitbrush
N. cinerea orolestes, July

Chrysothamnus viscidiflorus pumilus (Nutt.) H. and C.
N. cinerea arizonae, Aug.

Coleogyne ramosissima Torr. Blackbush
N. mexicana inopinata, June
N. albigula brevicauda, June

Cornus stolonifera Michx. Red-osier dogwood
N. cinerea orolestes, July

Cowania mexicana Don. Cliffrose
N. mexicana inopinata, June

Crataegus sp. Hawthorn
N. cinerea orolestes, Oct.

Ephedra torreyana Wats. Torrey jointfir
N. mexicana inopinata, June

Ephedra viridis Coville. Mormon tea
N. cinerea arizonae, Aug., Sept.
N. mexicana inopinata, Aug., Nov.
N. albigula laplataensis, Sept.

Eriogonum simpsoni Benth. Slender buckwheat
N. mexicana inopinata, Oct.

Eurotia lanata (Pursh) Moq. Winterfat
N. cinerea orolestes, July, Sept.
N. mexicana fallax, Sept.
N. mexicana inopinata, Sept.
N. albigula laplataensis, Aug., Nov.

Fendlera rupicola A. Gray. Fendlera
N. mexicana inopinata, June
N. albigula laplataensis, Oct.

Forestiera neomexicana A. Gray. Paloblanco.
N. mexicana inopinata, June

Grayia spinosa (Hook.) Moq. Spiny hop-sage
N. cinerea arizonae, Aug.

Gutierrezia sarothrae (Pursh) Brit. and Rusby. Broom snakeweed
N. cinerea arizonae, Aug.
N. mexicana scopulorum, May
N. mexicana inopinata, Aug.
N. lepida sanrafaeli, Sept.

Gutierrezia sarothrae microcephala (DC.) Benson
N. albigula laplataensis, Sept.

Gutierrezia. Snakeweed
(Records other than as reported under species of *Gutierrezia*)
N. cinerea arizonae, Sept., Oct.
N. mexicana fallax, Sept.
N. mexicana inopinata, June, Oct.
N. albigula warreni, May
N. floridana campestris, May, Nov.
N. lepida sanrafaeli, Nov.

Holodiscus dumosus (Nutt.) Heller. Creambush
N. cinerea orolestes, July, Aug.

Juniperus communis L. Mountain common juniper
N. cinerea orolestes, July

Lonicera involucrata (Richardson) Banks. Twinberry honeysuckle
N. cinerea orolestes, July, Aug.

Lycium pallidum Miers, Pale desert-thorn
N. cinerea arizonae, Oct.
N. albigula laplataensis, Aug., Sept., Nov.

Mimosa borealis A. Gray. Mimosa
N. albigula warreni, May

Pachystima myrsinites (Pursh) Raf. Mountain lover
N. cinerea orolestes, June, July, Aug., Sept.

Peraphyllum ramosissimum Nutt. Squaw-apple
N. mexicana inopinata, Aug.

- *Prunus virginiana* L. Chokecherry
  - *N. cinerea orolestes,* July, Aug., Sept., Oct., Nov.
  - *N. cinerea rupicola,* June
  - *N. mexicana fallax,* Aug., Sept.
  - *N. mexicana inopinata,* June, Aug., Oct., Nov.
  - *N. floridana campestris,* June
- *Ptelea baldwinii* T. and G. Hoptree
  - *N. micropus canescens,* May
- *Purshia tridentata* (Pursh) DC. Antelope brush
  - *N. cinerea orolestes,* Sept.
  - *N. cinerea arizonae,* Aug.
  - *N. mexicana inopinata,* Aug.
- *Quercus gambellii* Nutt. Scrub oak
  - *N. cinerea orolestes,* Sept.
  - *N. cinerea arizonae,* Aug., Sept.
  - *N. mexicana fallax,* Aug., Sept.
  - *N. mexicana inopinata,* June, Aug., Sept., Oct., Nov.
  - *N. albigula laplataensis,* Aug., Oct., Nov.
- *Quercus undulata* Torr. Wavyleaf oak
  - *N. albigula warreni,* May
  - *N. micropus canescens,* May
- *Rhus radicans* L. Western poison-ivy
  - *N. cinerea orolestes,* Oct.
  - *N. floridana campestris,* June
- *Rhus trilobata* Nutt. Skunkbush
  - *N. cinerea orolestes,* July, Aug., Nov.
  - *N. cinerea arizonae,* Aug., Sept., Oct.
  - *N. cinerea rupicola,* June
  - *N. mexicana fallax,* Sept.
  - *N. mexicana scopulorum,* May
  - *N. mexicana inopinata,* June, Aug., Oct., Nov.
  - *N. albigula warreni,* May
  - *N. floridana campestris,* May, June, Nov.
- *Ribes aureum* Pursh. Golden currant
  - *N. mexicana inopinata,* June
  - *N. floridana campestris,* June
- *Ribes cereum* Dougl. Squaw currant
  - *N. cinerea orolestes,* July, Aug.
  - *N. mexicana fallax,* Aug., Nov.
  - *N. micropus canescens,* May
- *Ribes inerme* Rydb. Whitestem gooseberry
  - *N. cinerea orolestes,* July
  - *N. cinerea arizonae,* Aug.
  - *N. mexicana inopinata,* Aug.
- *Ribes* (*Grossularia*). Gooseberry
  - (Records other than as reported under *R. aureum* and *R. inerme*)
  - *N. cinerea orolestes,* Aug.
  - *N. cinerea arizonae,* Sept.
  - *N. mexicana fallax,* Sept.
- *Rosa nutkana* Presl. Nootka rose
  - *N. cinerea orolestes,* July, Sept.
  - *N. floridana campestris,* June
- *Rosa woodsii* Lindl. Woods rose
  - *N. cinerea orolestes,* July
- *Rosa.* Rose
  - (Records other than as reported under *R. nutkana* and *R. woodsii*)
  - *N. cinerea* orolestes, Aug., Oct., Nov.
  - *N. cinerea arizonae,* Sept.
  - *N. mexicana inopinata,* June, Aug.
- *Rubus deliciosus* Torr. Thimbleberry
  - *N. mexicana fallax,* Aug.
- *Rubus strigosus* Michx. Wild red raspberry
  - *N. cinerea orolestes,* July
- *Salix.* Willow
  - *N. cinerea orolestes,* July, Nov.
- *Sambucus pubens* Michx. Red elderberry
  - *N. cinerea orolestes,* July, Aug.
- *Sarcobatus vermiculatus* (Hook.) Torrey. Greasewood
  - *N. cinerea arizonae,* Aug., Oct.
  - *N. mexicana inopinata,* Sept.
  - *N. albigula laplataensis,* Sept.
  - *N. floridana campestris,* May
  - *N. lepida sanrafaeli,* Nov.
- *Symphoricarpos occidentalis* Hook. Wolfberry
  - *N. floridana campestris,* June
- *Symphoricarpos utahensis* Rydb. Utah snowberry
  - *N. cinerea orolestes,* July, Aug.

Symphoricarpos. Snowberry
(Records other than as reported under species of *Symphoricarpos*)
- *N. cinerea orolestes,* Aug., Sept., Oct.
- *N. mexicana fallax,* Aug., Sept.
- *N. mexicana inopinata,* Aug.

Tetradymia spinosa H. and A. Cottonthorn
- *N. cinerea arizonae,* Sept.
- *N. albigula laplataensis,* Sept.

Yucca cf. *Y. angustissima* Engelm. Narrowleaf yucca
- *N. cinerea orolestes,* July
- *N. cinerea arizonae,* Sept., Oct.
- *N. mexicana inopinata,* Nov.
- *N. albigula brevicauda,* June
- *N. lepida sanrafaeli,* Nov.

Yucca baccata Torr. Spanish bayonet
- *N. cinerea arizonae,* Sept.
- *N. mexicana inopinata,* Aug., Sept.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Sept.

Yucca glauca Nutt. Soapweed
- *N. cinerea orolestes,* May, Aug.
- *N. mexicana fallax,* Nov.
- *N. mexicana scopulorum,* May
- *N. albigula warreni,* May
- *N. micropus canescens,* May
- *N. floridana campestris,* May, June, Nov.

Yucca cf. *Y. standleyi* McKelvey.
- *N. albigula warreni,* May

CACTI

Echinocactus whipplei Engelm. and Bigel. Braided arrow
- *N. cinerea arizonae,* Oct.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Aug., Sept., Nov.

Echinocereus coccineus Engelm. Bunch-ball cactus
- *N. mexicana inopinata,* Aug.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Aug., Sept., Nov.

Echinocereus triglochidiatus Engelm. King's crown cactus
- *N. cinerea arizonae,* Aug.

Mammillaria vivipara (Nutt.) Haworth. Common pincushion
- *N. cinerea orolestes,* July
- *N. albigula laplataensis,* Sept.

Opuntia arborescens Engelm. Tree cactus
- *N. mexicana fallax,* Sept.
- *N. mexicana scopulorum,* May
- *N. albigula warreni,* May
- *N. micropus canescens,* May, June
- *N. floridana campestris,* May

Opuntia davisii Engelm. and Bigel. Rat-tail cactus
- *N. cinerea arizonae,* Sept.
- *N. mexicana inopinata,* June, Oct.
- *N. albigula laplataensis,* Aug., Sept., Oct.

Opuntia fragilis (Nutt.) Haworth. Brittle cactus
- *N. cinerea orolestes,* Nov.
- *N. mexicana inopinata,* Aug.

Opuntia hystricina Engelm. and Bigel. Porcupine cactus
- *N. cinerea arizonae,* Oct.
- *N. albigula laplataensis,* Aug., Sept.

Opuntia phaeacantha Engelm. New Mexican prickly pear
- *N. mexicana inopinata,* Aug., Oct.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Sept.
- *N. albigula warreni,* May
- *N. micropus canescens,* June

Opuntia polyacantha Haworth. Hunger cactus
- *N. cinerea orolestes,* May, July, Sept., Nov.
- *N. cinerea arizonae,* Aug.
- *N. cinerea rupicola,* June
- *N. mexicana fallax,* Nov.
- *N. mexicana inopinata,* Aug., Sept., Oct., Nov.
- *N. albigula brevicauda,* June
- *N. albigula laplataensis,* Aug., Sept.

- *N. albigula warreni,* May
- *N. micropus canescens,* May
- *N. floridana campestris,* May, Nov.
- *N. lepida sanrafaeli,* Sept., Nov.

Opuntia humifusa Raf.
- *N. mexicana fallax,* Sept.
- *N. mexicana scopulorum,* May
- *N. albigula warreni,* May
- *N. micropus canescens,* June
- *N. floridana campestris,* May

Opuntia rhodantha Schumann. Wide cactus
- *N. cinerea arizonae,* Aug.?, Nov.
- *N. mexicana inopinata,* June, Oct., Nov.
- *N. albigula laplataensis,* June, Sept., Oct., Nov.
- *N. lepida sanrafaeli,* Nov.

Vines

Clematis columbiana (Nutt.) Torr. and Gray
- *N. cinerea orolestes,* Sept.

Clematis ligusticifolia Nutt. Virgin's bower
- *N. cinerea arizonae,* Aug.
- *N. mexicana inopinata,* June, Oct.

Cucurbita foetidissima H. B. K. Wild gourd
- *N. floridana campestris,* May

Humulus americanus Nutt. Hop
- *N. cinerea orolestes,* Oct.

Vitis sp. Grape
- *N. floridana campestris,* June

Grasses

Agropyron cf. *A. trachycaulum* (Link) Malte. Slender wheatgrass
- *N. cinerea orolestes,* Aug.

Agrostis sp. Bentgrass
- *N. mexicana inopinata,* Oct.

Bouteloua gracilis (H. B. K.) Lag. Blue grama
- *N. mexicana inopinata,* Aug.
- *N. albigula warreni,* May
- *N. micropus canescens,* June
- *N. floridana campestris,* May

Bouteloua. Grama
- (Records other than as reported under *B. gracilis*)
- *N. lepida sanrafaeli,* Nov.

Bromus tectorum L. Downy chess
- *N. albigula laplataensis,* Aug. Nov.

Bromus. Bromegrass
- (Records other than as reported under *B. tectorum*)
- *N. cinerea orolestes,* Sept.
- *N. mexicana inopinata,* Oct.

Elymus macounii Vasey. Macoun wild-rye
- *N. albigula laplataensis,* Sept.

Elymus. Wild-rye
- (Records other than as reported under *E. macounii*)
- *N. cinerea orolestes,* July

Hilaria jamesii (Torr.) Benth. Galleta
- *N. albigula brevicauda,* June

Muhlenbergia racemosa (Michx.) B. S. P. Marsh muhly
- *N. mexicana inopinata,* Oct.

Panicum virgatum L. Switchgrass
- *N. mexicana scopulorum,* May

Sporobolus airoides (Torr.) Torr. Alkali sacaton
- *N. cinerea arizonae,* Sept.
- *N. floridana campestris,* May

Sporobolus cryptandrus (Torr.) Gray. Sand dropseed
- *N. mexicana scopulorum,* May
- *N. albigula warreni,* May

Tridens elongatus (Buckl.) Nash. Rough tridens
- *N. albigula warreni,* May

FORBS

Achillea lanulosa Nutt. Yarrow
  N. mexicana inopinata, Nov.
Allium sp. Onion
  N. mexicana fallax, Aug.
Amaranthus albus L. Pigweed
  N. cinerea arizonae, Sept.
  N. albigula warreni, May
  N. floridana campestris, June
Amaranthus retroflexus L. Redroot pigweed
  N. albigula warreni, May
Ambrosia coronopifolia T. and G. Perennial ragweed
  N. albigula warreni, May
Ambrosia. Ragweed
  (Records other than as reported under *A. coronopifolia*)
  N. cinerea rupicola, June
  N. floridana campestris, May
Anemone globosa Nutt. Red anemone
  N. cinerea orolestes, July
Arctium minus (Hill) Bernh, Burdock
  N. cinerea orolestes, Nov.
Argemone platyceras hispida (Gray) Prain. Prickly poppy
  N. albigula warreni, May
Artemisia dracunculus glauca (Pallas) H. and C. Silky wormwood
  N. cinerea orolestes, Aug.
  N. mexicana inopinata, Oct.
Artemisia ludoviciana Nutt. Mugwort
  N. cinerea arizonae, Aug.
  N. cinerea rupicola, June?
  N. mexicana fallax, Sept., Nov.
  N. mexicana scopulorum, May
  N. mexicana inopinata, June, Aug., Oct.
  N. albigula warreni, May
  N. floridana campestris, May, June?
Asclepias arenaria Torr. Sand milkweed
  N. albigula warreni, May
Asclepias latifolia (Torr.) Raf. Green broadleaved milkweed
  N. albigula warreni, May
  N. micropus canescens, June
Asclepias sp. Milkweed
  (Records other than as reported under *A. arenaria* and *A. latifolia*)
  N. mexicana scopulorum, May
Aster arenosus Blake
  N. mexicana inopinata, Aug.
Aster glaucodes Blake
  N. cinerea orolestes, Aug.
Aster rubrotinctus Blake (a complex)
  N. cinerea orolestes, Aug., Sept.
Aster. Aster
  (Records other than as reported under species of *Aster*)
  N. cinerea orolestes, July
  N. mexicana inopinata, Nov.
Astragalus cf. *A. pectinatus* (Hook.) Dougl. Comb-leaf loco
  N. mexicana scopulorum, May
Astragalus racemosus Pursh. Stout leafy loco
  N. albigula laplataensis, Sept.
Astragalus tenellus Pursh. Looseflower milkvetch
  N. cinerea orolestes, July
Astragalus. Milkvetch
  (Records other than as reported under species of *Astragalus*)
  N. cinerea orolestes, Sept.
  N. mexicana fallax, Aug.
  N. albigula warreni, May
Barbarea sp. Wintercress
  N. cinerea orolestes, Sept.
Berberis fendleri A. Gray. Fendler barberry
  N. mexicana inopinata, Aug., Oct., Nov.
Berberis repens Lindl. Oregon grape
  N. cinerea orolestes, July, Aug.
  N. mexicana fallax, Aug.
  N. mexicana inopinata, Aug., Nov.
Chenopodium incanum (S. Wats.) A. Heller. Mealy goosefoot
  N. mexicana inopinata, Aug.
  N. albigula laplataensis, Sept.

Chenopodium rubrum L.
Red goosefoot
N. cinerea orolestes, Aug.
Chenopodium. Goosefoot
(Records other than as reported under *C. incanum* and *C. rubrum*)
N. cinerea orolestes, July, Sept.
N. cinerea rupicola, June
N. mexicana inopinata, Oct.
Chrysopsis foliosa Nutt.
N. mexicana fallax, Sept.
Chrysopsis villosa (Pursh) Nutt.
Hairy goldaster
N. cinerea orolestes, July
N. mexicana inopinata, June
N. albigula laplataensis, June
Chrysopsis. Goldaster
(Records other than as reported under *C. foliosa* and *C. villosa*)
N. cinerea arizonae, Aug.
N. mexicana inopinata, Aug., Sept., Oct.
N. albigula laplataensis, Aug.
Cirsium. Thistle
N. cinerea orolestes, July, Oct.
N. mexicana scopulorum, May
N. mexicana inopinata, Oct.
N. albigula warreni, May
Conyza canadensis (L.) Cronq.
N. mexicana fallax, Sept.
N. mexicana inopinata, Oct.
Cryptantha fendleri (Gray) Greene. Nievitas
N. cinerea orolestes, July
Dalea aurea Nutt.
N. albigula warreni, May
Delphinium. Larkspur
N. cinerea orolestes, July
N. mexicana fallax, Aug.
Epilobium angustifolium L. Fireweed.
N. cinerea orolestes, July
Eriogonum cernuum Nutt. Nodding eriogonum
N. cinerea orolestes, July
Eriogonum jamesii Benth. James' eriogonum
N. mexicana inopinata, Aug.
Eriogonum. Buckwheat
(Records other than as reported under *E. cernuum* and *E. jamesii*)
N. cinerea arizonae, Nov.
N. albigula warreni, May
N. lepida sanrafaeli, Nov.
Euphorbia serpyllifolia Pers.? Thyme-leaf spurge
N. albigula laplataensis, Sept.
Galium sp. Bedstraw
N. cinerea orolestes, Oct.
Gaura coccinea Nutt. Low gaura
N. mexicana inopinata, Oct.
Gaura villosa Torr. Hairy gaura
N. mexicana fallax, Sept.
Gentiana cf. *G. parryi* Engelm. Parry gentian
N. cinerea orolestes, July
Geranium fremontii cowenii (Rydb.) Harrington
N. cinerea orolestes, Sept.
Geranium richardsonii Fisch. and Trautv.
N. cinerea orolestes, Aug.
Geranium. Cranesbill
(Records other than as reported under *G. fremontii cowenii* and *G. richardsonii*)
N. cinerea orolestes, Nov.
Gnaphalium sp. Cudweed
N. cinerea orolestes, Sept.
Grindelia inornata angusta Steyermark
N. mexicana fallax, Sept.
Grindelia cf. *G. squarrosa* (Pursh) Dunal. Broad-leaved gumweed
N. floridana campestris, May
Helianthus annuus L.
Kansas sunflower
N. albigula warreni, May
N. floridana campestris, June, Nov.
Helianthus rigidus (Cass.) Desf.
Stiff sunflower
N. mexicana fallax, Nov.

Helianthus. Sunflower
(Records other than as reported under *H. annuus* and *H. rigidus*)
N. mexicana scopulorum, May
Heracleum lanatum Michx. Cow parsnip
N. cinerea orolestes, July
Heuchera parvifolia Nutt. Small-leaved alumroot
N. cinerea orolestes, Sept.
Hymenopappus lugens Greene?
N. mexicana inopinata, June
Hymenoxys acaulis ivesiana (Greene) Parker. Actinea
N. mexicana inopinata, June
Hymenoxys richardsonii (Hook.) Ckll.
N. cinerea orolestes, July
N. albigula laplataensis, Aug., Nov.
Iva axillaris Pursh. Mouse-ear povertyweed
N. cinerea orolestes, Sept.
Iva xanthifolia Nutt. False ragweed
N. mexicana fallax, Sept.
Kuhnia eupatorioides L. False boneset
N. albigula warreni, May
N. floridana campestris, Nov.
Lappula redowskii (Hornem.) Greene. Stickseed
N. cinerea rupicola, June
Lathyrus. Sweet pea
N. cinerea orolestes, Aug.
N. mexicana fallax, Sept.
N. mexicana inopinata, Aug.
Lepidium montanum Nutt.
N. mexicana inopinata, June, Aug., Oct.
N. lepida sanrafaeli, Nov.
Lepidium lasiocarpum Nutt.
N. cinerea arizonae, Oct.
Lepidium. Peppergrass
(Records other than as reported under *L. lasiocarpum* and *L. montanum*)
N. cinerea orolestes, July
N. albigula laplataensis, Sept.
Lesquerella fendleri (A. Gray) S. Wats.
N. albigula warreni, May
Lesquerella ovalifolia Rydb. Oval-leaved bladderpod
N. albigula warreni, May
Lesquerella sp. Bladderpod
(Record other than as reported under *L. fendleri* and *L. ovalifolia*)
N. mexicana fallax, Sept.
Liatris punctata Hook. Gayfeather
N. albigula warreni, May
Lithospermum sp. Puccoon
N. cinerea orolestes, Sept.
Lupinus. Lupine
N. cinerea orolestes, Sept.
N. albigula brevicauda, June
Marrubium vulgare L. Hoarhound
N. cinerea orolestes, Nov.
N. mexicana inopinata, Aug., Oct.
N. albigula laplataensis, Nov.
N. micropus canescens, May
Melilotus alba Desr. White sweetclover
N. mexicana fallax, Sept.
Melilotus officinalis (L.) Lam. Yellow sweetclover
N. albigula laplataensis, Oct.
Melilotus. Sweetclover
(Records other than as reported under *M. alba* and *M. officinalis*)
N. cinerea orolestes, Nov.
N. mexicana inopinata, Oct.
N. albigula laplataensis, June
Mentzelia decapetala (Pursh) Urban and Gilg. Large evening star
N. floridana campestris, June
Mentzelia. Evening star
(Records other than as reported under *M. decapetala*)
N. cinerea rupicola, June
N. albigula warreni, May
N. floridana campestris, May
Mirabilis linearis (Pursh) Heimerl.
N. albigula laplataensis, Oct.
N. lepida sanrafaeli, Sept.

Mirabilis multiflora (Torr.) Gray. Showy four-o'clock
  N. cinerea arizonae, Sept.
  N. albigula brevicauda, June
  N. albigula laplataensis, Oct.
Mirabilis oxybaphoides A. Gray
  N. mexicana inopinata, Oct.
Mirabilis sp. Four-o'clock
  (Record other than as reported under species of *Mirabilis*)
  N. mexicana fallax, Sept.
Oenothera coronopifolia T. and G.
  N. cinerea orolestes, July
Oenothera lavandulaefolia T. and G.
  N. albigula warreni, May
Onosmodium. Marbleseed
  N. mexicana fallax, Aug., Sept.
Orthocarpus sp. Owlclover
  N. cinerea orolestes, Sept.
Penstemon bridgesii A. Gray
  N. cinerea arizonae, Aug.
Penstemon. Beardtongue
  (Records other than as reported under *P. bridgesii*)
  N. mexicana inopinata, June, Aug., Sept.
  N. albigula laplataensis, Aug., Sept.
Physalis. Ground cherry
  N. cinerea arizonae, Sept.
  N. mexicana inopinata, Sept.
  N. albigula laplataensis, Sept., Oct.
  N. albigula warreni, May
Polanisia trachysperma T. and G. Clammy-weed
  N. micropus canescens, May
Polygonum sp. Knotweed
  N. cinerea orolestes, July
Potentilla gracilis Dougl. Goldcup
  N. cinerea orolestes, Oct.
Potentilla hippiana Lehm. Wooly cinquefoil
  N. cinerea orolestes, Oct.
Potentilla sp. Cinquefoil
  (Record other than as reported under *P. gracilis* and *P. hippiana*)
  N. cinerea orolestes, Aug.
Psoralea linearifolia T. and G. Scurf-pea
  N. cinerea rupicola, June
  N. albigula warreni, May
  N. floridana campestris, June
Ratibida columnifera (Nutt.) Wooton and Stand. Long-headed coneflower
  N. albigula warreni, May
Ratibida tagetes (James) Barnh. Short-rayed coneflower
  N. mexicana scopulorum, May
Salsola kali L. Russian thistle
  N. cinerea orolestes, July, Sept.
  N. cinerea arizonae, Sept., Oct., Nov.
  N. cinerea rupicola, June
  N. mexicana scopulorum, May
  N. mexicana inopinata, June, Aug., Oct., Nov.
  N. albigula brevicauda, June
  N. albigula laplataensis, Aug., Sept.
  N. albigula warreni, May
  N. micropus canescens, May, June
  N. floridana campestris, May
  N. lepida sanrafaeli, Sept., Nov.
Scrophularia lanceolata Pursh. Figwort
  N. cinerea orolestes, Aug.
Sedum integrifolium (Raf.) A. Nels. King's crown
  N. cinerea orolestes, July
Senecio longilobus Benth. Felty groundsel
  N. cinerea arizonae, Oct.
Senecio spartioides T. and G. Grass-leaved senecio
  N. cinerea orolestes, Oct.
  N. mexicana scopulorum, May
  N. floridana campestris, June
Senecio. Groundsel
  (Records other than as reported under *S. longilobus* and *S. spartioides*)
  N. cinerea orolestes, Aug.
  N. albigula warreni, May

Sisymbrium. Hedge mustard
  N. cinerea rupicola, June
Smilacina racemosa (L.) Desf. Feather solomonplume
  N. cinerea orolestes, Aug.
  N. mexicana inopinata, Aug.
Smilacina stellata (L.) Desf. Starry solomonplume
  N. cinerea orolestes, July, Aug., Sept.
Smilacina. Solomonplume
  (Records other than as reported under S. *racemosa* and S. *stellata*)
  N. cinerea orolestes, Oct.
  N. albigula laplataensis, Aug.
Solanum elaeagnifolium Cav. Blue potato-weed
  N. mexicana scopulorum, May
Solanum rostratum Dunal. Buffalo-bur
  N. albigula warreni, May
Solidago missouriensis Nutt.?
  N. cinerea orolestes, July
Solidago sparsiflora A. Gray
  N. cinerea orolestes, July
Solidago. Goldenrod
  (Records other than as reported under species of *Solidago*)
  N. cinerea orolestes, Aug., Oct.
Sphaeralcea coccinea elata (Baker) Kearney. Cowboy's delight
  N. mexicana inopinata, Oct.
Sphaeralcea parvifolia A. Nels.
  N. mexicana inopinata, June, Oct.
Sphaeralcea. Globe mallow
  (Records other than as reported under species of *Sphaeralcea*)
  N. albigula laplataensis, Aug.
  N. micropus canescens, June
Stanleya albescens M. E. Jones. White bottlebrush
  N. cinerea arizonae, Nov.
  N. mexicana inopinata, Nov.
Stanleya pinnata (Pursh) Britt. Princesplume
  N. mexicana inopinata, June
  N. floridana campestris, May
Stanleya
  (Records other than as reported under S. *albescens* and S. *pinnata*)
  N. cinerea orolestes, Sept.
Streptanthus cordatus Nutt. Twist-flower
  N. lepida sanrafaeli, Nov.
Thermopsis. Goldenpea
  N. mexicana fallax, Aug.
Tragopogon sp. Salsify
  N. mexicana fallax, Sept.
Valeriana edulis Nutt. Valerian
  N. cinerea orolestes, July
Verbascum thapsus L. Mullein
  N. mexicana inopinata, Oct.
Verbena sp. Vervain
  N. mexicana scopulorum, May
Xanthium. Cocklebur
  N. mexicana scopulorum, May
  N. albigula laplataensis, Oct.
  N. micropus canescens, May

FUNGI

Agaricaceae. unidentified mushrooms.
  N. cinerea orolestes, June, July, Aug., Sept.
Lycoperdaceae. unidentified puffball.
  N. albigula warreni, May

Every kind of tree and shrub seen growing within 100 feet of each den was identified at least to genus. Hence the data presented in tables of food plants in the following accounts, showing the percentages of use to availability of each plant, should be almost complete for the woody plants, which are of major importance as food of wood rats.

Special attention was given in the field to the identification of species of cactus, because of their importance as food and because of the difficulty of preparing satisfactory specimens for herbarium study. The identifications of cacti are based primarily on "Colorado Cacti" by Boissevain and Davidson, 1940, but the nomenclature has been modified to conform with that of Harrington, 1954. In spite of considerable attention given to the study of the Cactaceae by various authors over the years, the taxonomy of this family remains in a highly unsatisfactory state of affairs. Boissevain and Davidson's comments are indicative when they say (*op. cit.*: 18) concerning the dry-fruited platyopuntias in Colorado, "They present an immense diversity of form and all kinds of transitional forms between the species" and ". . . we have found in almost every valley an *Opuntia* that is slightly different from those in the neighboring valleys. . . ." "We have recognized as species those forms that occur most abundantly and have the widest range." From my own field observations I believe the following forms to be conspecific: *Opuntia schweriniana* Schumann, *O. hystricina* Engelmann and Bigelow, *O. rhodantha* Schumann, *O. trichophora* (Engelmann and Bigelow) Britton and Rose, and *O. polyacantha* Haworth. But much careful field study, collection of formaldehyde specimens, and rearing of plants needs to be done before the correct names and relationships of this complex, intergrading, and perhaps hybridizing group can be determined for certain.

In analyzing the food litter, effort was made to identify the cuttings and other debris of every kind of forb eaten, as far as possible. But at most of the dens only the more abundant or conspicuous forbs available but untouched were identified. If every kind of forb available had been recorded, the percentage figures in tables of food plants indicating relative preference would be lower for most of the less important forbs, and more kinds would be listed that were not known to be eaten. On the other hand, even if absolutely complete and accurate for all plants, the figures would not give a full and true picture of the food preferences of the wood rat, because small tender forbs brought to the den may be entirely consumed without leaving a trace in the food litter, and much food is certainly eaten where it is encountered on sorties away from the den (see page 388). Nevertheless it is considered that these sources of error do not seriously affect the more important food plants, most of which are conspicuous in the field and remain easily recognizable in the food litter.

The data obtained for grasses is extremely meager, especially in comparison with the abundance of grasses in many habitats. Grass debris seldom appeared in food litter or storage and only scattered in small amounts. No stored grass seeds were found. It is possible that wood rats foraging away from their dens eat much green grass and seeds in favorable seasons, but probably little is carried back to the dens. The meagerness of the data for grasses is also, in part, due to the meager attention devoted to them in the field. It did not seem wise to concentrate more effort studying and collecting a group of plants of so little importance in the lives of wood rats.

The emphasis placed by Bailey (1931: 179, 184, 190) on kinds of wild fruits and human camp supplies as foods of species of wood rats in New Mexico seems not to do justice to the importance of foliage, fresh or dry, in the diet of nearly all kinds of wood rats at all seasons of the year. The same kinds of rats in Colorado subsist mainly on leafy vegetation, conifer needles, and cactus, with seeds, nuts, and other fruits as supplements or temporary foods, which may at times be eaten in large amount.

Bones ranging in size from those of mice to those of deer are collected, sometimes in large numbers, by wood rats. *N. cinerea* seems to gather more bones than any other kind of wood rat in Colorado. Although the bones may serve primarily as building material for the dens, they are also extensively gnawed, sometimes until half of the bone or more has been consumed. Whether the gnawing is done primarily to keep the incisors in good condition or to obtain calcium and other elements for the diet cannot be said with certainty, but the former benefit seems to me more important.

PARASITES

Although parasites sometimes seriously affect the lives of individual wood rats, parasites are not known to be a significant factor in the distribution of any subspecies in Colorado. Only rarely did any rat that I studied seem to be so heavily infested with parasites that its health was impaired. Most kinds of ectoparasites collected are common to many, if not all, kinds of wood rats that occur in the same part of the state. Some of the parasites, such as the squirrel flea, *Diamanus montanus,* occur only sporadically on wood rats and normally are found on some other kind of animal.

Almost every wood rat obtained harbored at least a few ectoparasites. But samples of these were preserved only from individual hosts selected to represent each kind of rat and each part of the state in which field work was done. If parasites were numerous, no attempt was made to collect all those on a rat or to determine the relative or absolute numbers. The kinds of parasites that I collected from wood rats in Colorado include 5 ticks, 15 larval chiggers, 8 other mites, 2 lice, 1 cone-nosed bug, 1 warble fly, and 11 fleas. Three of the chiggers have been newly named and described from specimens collected in this study. Not all of the other parasites have been identified to species.

List of Parasites from Wood Rats in Colorado

ACARINA

Ixodidae

- *Dermacentor andersoni* Stiles
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea arizonae*
  - *Neotoma mexicana fallax*
  - *Neotoma mexicana inopinata*
- *Ixodes spinipalpis* Hadwen and Nuttall
  - *Neotoma cinerea rupicola*
  - *Neotoma mexicana fallax*
  - *Neotoma mexicana inopinata*
- *Ixodes woodi* Bishopp
  - *Neotoma cinerea orolestes*
  - *Neotoma mexicana inopinata*
- *Ixodes* sp. near *I. ochotonae* Gregson
  - *Neotoma cinerea rupicola*
- *Ixodes* sp.
  - *Neotoma albigula warreni*

Argasidae

- *Ornithodorus* sp.
  - *Neotoma cinerea orolestes*

Laelaptidae

- *Brevisterna utahensis* (Ewing)
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea rupicola*
  - *Neotoma albigula laplataensis*
  - *Neotoma albigula warreni*
  - *Neotoma floridana campestris*
  - *Neotoma lepida sanrafaeli*
- *Eubrachylaelaps circularis* (Ewing)
  - *Neotoma mexicana inopinata*
- *Euhaemogamasus ambulans* (Thorell)
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea arizonae*
- *Eviphis* sp.
  - *Neotoma mexicana fallax*
- *Haemolaelaps geomys* Strandtmann
  - *Neotoma cinerea orolestes*
- *Haemolaelaps glasgowi* (Ewing)
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea rupicola*
  - *Neotoma mexicana inopinata*
  - *Neotoma micropus canescens*
  - *Neotoma floridana campestris*

Dermanyssidae

- *Hirstionyssus neotomae* Eads
  - *Neotoma cinerea orolestes*
- *Hirstionyssus* cf. *H. otomys* (Radford)
  - *Neotoma mexicana inopinata*

Trombiculidae

Acomatacarus micheneri Greenburg
  Neotoma cinerea orolestes
  Neotoma cinerea arizonae
Leeuwenhoekia americana (Ewing)
  Neotoma cinerea orolestes
  Neotoma cinerea arizonae
  Neotoma mexicana inopinata
Euschöngastia criceticola Brennan
  Neotoma cinerea orolestes
  Neotoma cinerea arizonae
  Neotoma mexicana inopinata
  Neotoma albigula warreni
  Neotoma micropus canescens
  Neotoma floridana campestris
  Neotoma lepida sanrafaeli
Euschöngastia guntheri (Radford)
  Neotoma cinerea orolestes
Euschöngastia lacerta Brennan
  Neotoma cinerea orolestes
  Neotoma cinerea arizonae
  Neotoma mexicana inopinata
  Neotoma albigula laplataensis
Euschöngastia finleyi Crossley
  Neotoma cinerea arizonae
  Neotoma mexicana inopinata
  Neotoma lepida sanrafaeli
Euschöngastia hoffmannae Gould
  Neotoma mexicana inopinata
Trombicula (Eutrombicula) alfreddugesi Oudemans
  Neotoma cinerea orolestes
  Neotoma cinerea arizonae
  Neotoma mexicana fallax
  Neotoma albigula laplataensis
Trombicula (Neotrombicula) autumnalis (Shaw)
  Neotoma cinerea orolestes
Trombicula (Neotrombicula) finleyi Kardos
  Neotoma cinerea orolestes
Trombicula (Neotrombicula) harperi Ewing
  Neotoma cinerea orolestes
  Neotoma mexicana fallax
Trombicula (Neotrombicula) microti Ewing
  Neotoma cinerea orolestes
Trombicula arenicola Loomis
  Neotoma albigula warreni
Trombicula hoplai Loomis
  Neotoma mexicana inopinata (from New Mexico)
  Neotoma lepida sanrafaeli
Trombicula potosina Hoffman
  Neotoma cinerea arizonae
  Neotoma mexicana inopinata
  Neotoma albigula brevicauda
  Neotoma albigula laplataensis
  Neotoma lepida sanrafaeli

ANOPLURA

Haematopinidae

Neohaematopinus inornatus (Kellogg and Ferris)
  Neotoma cinerea orolestes
  Neotoma cinerea rupicola
  Neotoma mexicana inopinata
Neohaematopinus neotomae Ferris
  Neotoma albigula laplataensis
  Neotoma albigula warreni
  Neotoma micropus canescens
  Neotoma floridana campestris

HEMIPTERA

Reduviidae

Triatoma protracta (Uhler)
  Neotoma mexicana inopinata

Diptera

Cuterebridae

- *Cuterebra tenebrosa* Coq.
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea rupicola*

Siphonaptera

Hectopsyllidae

- *Echidnophaga gallinacea* (Westwood)
  - *Neotoma lepida sanrafaeli*

Hystrichopsyllidae

- *Anomiopsyllus* sp.
  - *Neotoma mexicana inopinata*
  - *Neotoma albigula laplataensis*
  - *Neotoma albigula warreni*
  - *Neotoma micropus canescens*
  - *Neotoma floridana campestris*
- *Hystrichopsylla* sp.
  - *Neotoma lepida sanrafaeli*
- *Megarthroglossus* sp.
  - *Neotoma cinerea orolestes*
  - *Neotoma mexicana fallax*
- *Phalacropsylla* sp.
  - *Neotoma cinerea orolestes*
- *Stenistomera alpina* (Baker)
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea rupicola*
  - *Neotoma mexicana scopulorum*
  - *Neotoma mexicana inopinata*
  - *Neotoma albigula warreni*
  - *Neotoma floridana campestris*

Ceratophyllidae

- *Diamanus montanus* (Baker)
  - *Neotoma mexicana fallax*
  - *Neotoma mexicana inopinata*
- *Malaraeus* sp.
  - *Neotoma cinerea orolestes*
  - *Neotoma mexicana inopinata*
  - *Neotoma albigula laplataensis*
  - *Neotoma albigula warreni*
  - *Neotoma micropus canescens*
  - *Neotoma floridana campestris*
  - *Neotoma lepida sanrafaeli*
- *Monopsyllus wagneri* (Baker)
  - *Neotoma cinerea orolestes*
- *Orchopeas sexdentatus* (Baker)
  - *Neotoma cinerea orolestes*
  - *Neotoma cinerea arizonae*
  - *Neotoma cinerea rupicola*
  - *Neotoma mexicana fallax*
  - *Neotoma mexicana inopinata*
  - *Neotoma albigula brevicauda*
  - *Neotoma albigula laplataensis*
  - *Neotoma micropus canescens*
  - *Neotoma floridana campestris*
  - *Neotoma lepida sanrafaeli*
- *Peromyscopsylla* sp.
  - *Neotoma mexicana inopinata*

Cestoda

Anoplocephalidae

- *Andrya* cf. *A. macrocephala* Douthitt
  - *Neotoma cinerea orolestes*

Taeniidae

- ?*Cladotaenia* sp.
  - *Neotoma albigula warreni*
- ?*Taenia* sp.
  - *Neotoma mexicana inopinata*

Ticks removed from wood rats were usually attached to the pinna, or unattached elsewhere. All ticks were in the larval or nymphal stages except two adult females of *Ixodes* (*I. woodi,* 491018-1, and *I. spinipalpis,* 491024-7). Chiggers were usually inside the ear or on the pinna. Less regularly a few were found on the face, rump, or other parts of the body. Frequently a single individual rat carried chiggers of more than one species, sometimes of three species belonging to two genera.

The lice collected are of two species that can be separated according to host species. Those from *N. cinerea* and *N. mexicana* are *Neohaematopinus inornatus* and those from *N. albigula, micropus,* and *floridana* are *Neohaematopinus neotomae.* Concerning these lice, Dr. G. F. Ferris wrote on 29 September 1952 as follows: "The two species are quite definitely distinct and the division seems to hold, for specimens from *cinerea* in California cannot be separated from those from *cinerea* in Colorado. Those from the other species differ a little bit among themselves but offer nothing that could be used to separate them into two or more species, and these include specimens from *fuscipes* in California."

Warbles were of frequent occurrence on wood rats in the summer and were usually situated on the throat, breast, or side of the neck. Probably all species of wood rats in Colorado are attacked by the warble fly. Only three full grown warbles were reared to maturity. These came from *Neotoma cinerea orolestes* and *N. cinerea rupicola* and have been identified as *Cuterebra tenebrosa* Coq. described from Colorado. *C. tenebrosa* has been considered by some entomologists to be a synonym of *C. approximata* Walker, described from British Columbia.

Considerably more than half of all the fleas collected were of the species *Orchopeas sexdentatus,* which was found on 10 of the 12 subspecies of wood rats. This flea was also the one found most abundantly on *N. fuscipes luciana* Hooper by Linsdale and Tevis (1951: 175).

Lists of the parasites found on each subspecies of wood rat are included in the ecological accounts of each species. Following the names of each parasite are the field numbers of each individual host. These numbers are also the original numbers by which the preserved parasites have been labeled. The dates of collection are indicated by the field numbers, which are based on a six-digit date group (year-month-day). Localities may be determined by reference to the same numbers under the sections on food, where the food plants at each den are recorded.

ECOLOGICAL ACCOUNTS OF SPECIES

Neotoma cinerea (Ord)

Bushy-tailed wood rat

HABITAT

The bushy-tailed wood rat tolerates a wide range of climatic conditions in western North America, from the cold winters of the northern Rocky Mountains to the hot semiarid summers of northern Arizona. Almost the full range of temperatures experienced by the species can be found in Colorado because of the great differences in elevation. *N. cinerea* is the only species of wood rat that has no altitudinal limits in Colorado. E. R. Warren (1942: 217) reported *N. c. orolestes* at the summit of Pikes Peak, 14,110 feet, in the Arctic-Alpine Life-zone. No other species occurs higher than 9000 feet in the upper part of the Transition Life-zone. Although the bushy-tailed wood rat does not reach its lower zonal limit in Colorado, the absence of this species from the Lower Sonoran Life-zone elsewhere indicates that *cinerea* does not endure high summer temperatures so well as do several other species.

The three subspecies of *N. cinerea* have somewhat different adaptations to climate. *N. c. orolestes* lives in the high mountains, primarily in the Transition, Canadian, and Hudsonian life-zones. In northwestern Colorado its range extends down into the Upper Sonoran, where the species is represented by a population showing intergradation with *arizonae*. *N. c. arizonae* occurs only in the Upper Sonoran Life-zone below an elevation of approximately 7500 feet. The range of this subspecies in western Colorado complements that of *orolestes*. *N. c. rupicola* has only a limited distribution in the Upper Sonoran Life-zone in northeastern Colorado. The lower limit of this subspecies is set by physiographic conditions, not climate. In Wyoming, the range of *rupicola* roughly complements that of *orolestes*, which lives in the higher mountains.

Dens of bushy-tailed wood rats occur in a wide variety of biotic communities, mostly of woodland or shrub type. Occasionally the rats occupy mountain grasslands when suitable rock shelter is present, but at least a few shrubs usually grow in such situations. The presence of wood rats is determined more by the kinds of rock shelter available than by the kinds of plant communities. Situations that provide adequate rock outcrops are likely to be associated with open forests of Douglas-fir, aspen, or ponderosa pine with numerous shrubs. At lower elevations piñons or junipers are usually present. The more common shrub communities include a mixture of shrubs growing among rocks and on open ground. Chokecherry, serviceberry, squaw currant, snowberry, mountain-mahogany, skunkbush, creambush, scrub oak, sagebrush, and rabbitbrush are common shrubs around wood rat dens. The dens are more likely to be abundant at the edge of a forest or in parkland than in the interior of a closed forest, probably because of the sparseness of the understory in closed forest. The differences in plant communities occupied by the three subspecies of *cinerea* are primarily a result of differences in elevation. Thus usually *arizonae*, alone, lives among junipers or piñons.

The numbers of dens examined in each kind of plant community and in each life-zone are presented in Table 2 for each subspecies.

TABLE 2.—LIFE-ZONES AND PLANT COMMUNITIES OF N. CINEREA

ZONE	Community	Numbers of dens		
		N. c. orolestes	*N. c. arizonae*	*N. c. rupicola*
Canadian	Bristlecone pine—Douglas-fir forest	1		
	Closed Douglas-fir forest	2		
	Douglas-fir—aspen	2		
	Open aspen—grassland	4		
	Montane grassland—mixed shrubs	1		
	Aspen—mixed shrubs	5		
	Creambush thicket—aspen	1		
	Chokecherry thicket—mixed shrubs	1		
Transition	Chokecherry thicket—mixed shrubs	1		
	Aspen—ponderosa pine	1		
	Open ponderosa pine—Douglas-fir forest	1		
	Scrub oak—ponderosa pine—Douglas-fir	1		
	Mixed shrubs—scattered pines	2		
	Cottonwood—willow	1		
	Mixed shrubs—sagebrush	5		
	Sage brush—scattered junipers	4		
	Sagebrush—rabbitbrush	1		
Upper Sonoran	Sagebrush—rabbitbrush	7		
	Piñon—juniper	1	4	
	Juniper—sagebrush		5	
	Greasewood—saltbush		1	
	Skunkbush—saltbush		1	
	Chokecherry—golden currant			4
	Totals	42	11	4

Topography and shelter are related aspects of the habitat having key significance for the existence of wood rats. All the dens of bushy-tailed wood rats seen in the course of this study were in some kind of rock formation or in some man-made structure that for a wood rat would be analogous to a cave or rock crevice. However, dens in other situations were found by Merrit Cary in western Moffat County (see p. 364).

The kind of shelter preferred by *N. cinerea* seems to be vertical crevices and clefts in cliffs or other high outcrops of rock. Caves are almost as well liked. These kinds of shelter are numerous only in rugged mountainous or canyon country such as predominates in the central and western parts of Colorado. Wherever high rock exposures exist in these parts of the state, *cinerea* is likely to be found. Where natural cliffs and caves are not abundant, this species is able to thrive by moving into mine tunnels, cabins, and other abandoned buildings. Such structures, unoccupied during at least part of the year, are prevalent in the high mountains and frequently shelter wood rats. Pueblo cliff dwellings provide excellent shelter for wood rats and probably were used prior to the departure of the Indians more than 600 years ago. Among the ruins of Mesa Verde, Cary (1911: 113) found rat fecal deposits blackened by the smoke from Indian fires.

Less desirable kinds of shelter sometimes used are horizontal clefts under rock outcrops, and spaces between and underneath fallen boulders or large rock blocks. Only the larger and more secure shelters of these types are likely to be occupied by *N. c. orolestes*. The den preferences of *arizonae* and *rupicola* are less clear-cut, perhaps because of the smaller size of the latter subspecies, which are able to get by with smaller den spaces. The choice of den rocks by *arizonae* is not actually as indifferent as indicated by my records of dens examined, for *arizonae* is the only wood rat known to inhabit some of the highest cliffs bordering mesas and canyons in western Colorado, where the dens were practically inaccessible.

The dens examined in each kind of shelter and in each kind of topography are presented in Table 3 for *N. c. orolestes* and in Table 4 for *N. c. arizonae*.

The dens of *N. c. rupicola*, from the High Plains rimrock and steep slope below, were situated in the following kinds of shelter:

Cave and fallen rocks	1 den
Vertical and horizontal crevices and boulders	1 den
Diagonal crevice through big sandstone block	1 den
Under big sandstone block	1 den

PLATE 11

FIG. 1. Mountain grassland and Engelmann spruce, with limestone outcrop sheltering dens of the bushy-tailed wood rat; view up West Lime Creek, six and a half miles southwest of Silverton, 10,100 feet elevation.

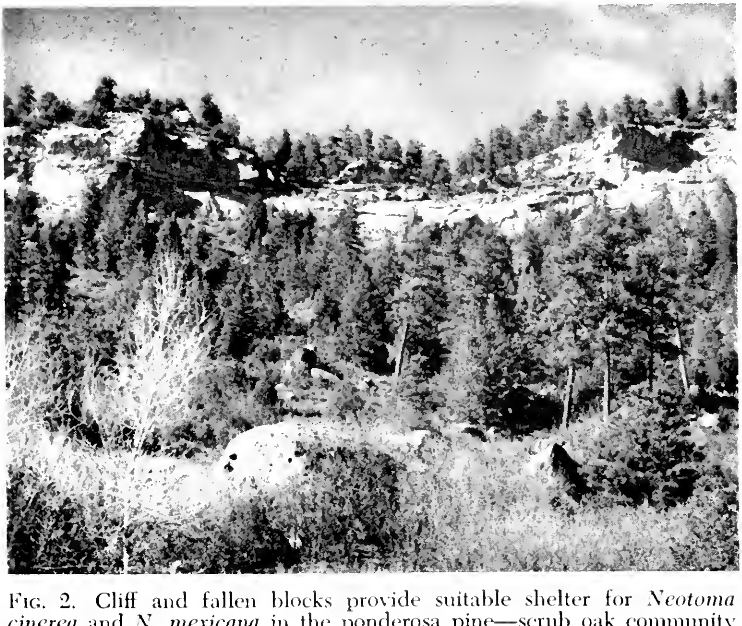


FIG. 2. Cliff and fallen blocks provide suitable shelter for *Neotoma cinerea* and *N. mexicana* in the ponderosa pine—scrub oak community southwest of Chromo, 7200 feet.

PLATE 12

FIG. 1. Rim of Cahone Canyon, 7000 feet, with piñon—juniper woodland and mixed shrubs. Dens of *N. cinerea* and *mexicana* are numerous under sandstone outcrops and large blocks.

FIG. 2. Nontypical habitat of *N. cinerea arizonae*; low broken sandstone rim of McElmo Creek, 4850 feet, in greasewood—saltbush community. View east toward Ute Peak.

PLATE 13

Fig. 1. Gold King Mill, 8 miles north and 1 mile west of Hesperus. The timbers, walls, and debris house many wood rat nests.

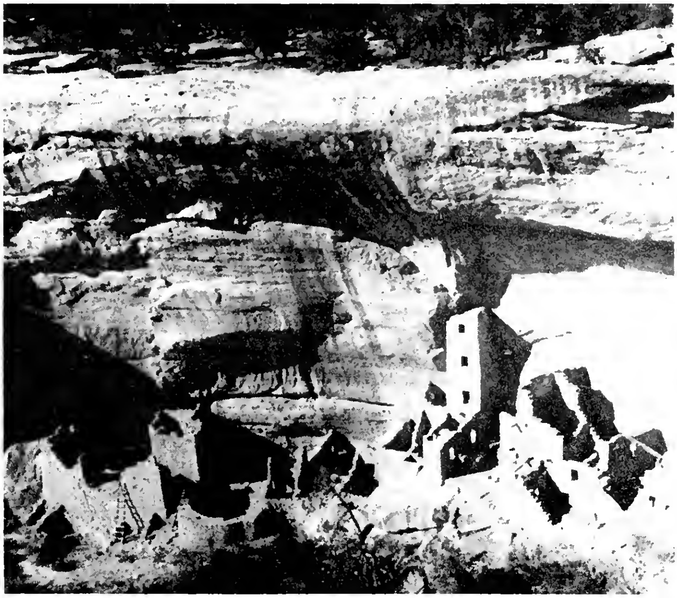


Fig. 2. Pueblo cliff dwellings, such as Square Tower House, Mesa Verde, provide favorable habitat for bushy-tailed and Mexican wood rats.

PLATE 14

FIG. 1. South end of sandstone cliff three miles north of Almont, 8300 feet. The large vertical clefts shelter dens of *N. cinerea orolestes.*

FIG. 2. South side of Fortification Rocks, 16 miles north of Craig. Crevices in the dike contain dens of *N. cinerea,* and the talus rocks below shelter a rattlesnake den.

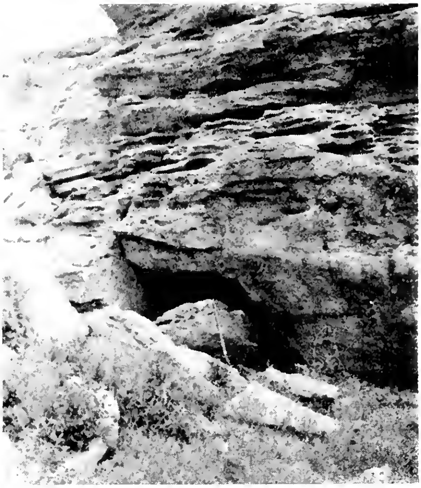


FIG. 3. Crevices and small cave sheltering *N. c. rupicola* (500602-1) in rim of High Plains, 21 miles north and 5 miles east of Stoneham.

TABLE 3.—SHELTER AND TOPOGRAPHY OF N. C. OROLESTES

SHELTER	Topography and number of dens							
	Cliff above steep slope	Cliff above moderate slope	Steep mountainside or canyon side	Abandoned gold mill on mountainside	Moderate rocky slope	Edge of valley bottom	Igneus dike on rolling hills	Totals
Vertical rock crevices	7	1	2	....	....	....	....	10
Vertical and horizontal crevices	3	....	....	....	1	....	2	6
Horizontal and diagonal crevices	....	....	1	....	....	....	....	1
Horizontal crevices	2	....	....	....	....	....	2	4
Crevices in and beneath rock overhang	2	....	....	....	....	....	1	3
Small cave and rock crevices	2	....	1	....	....	....	....	3
Walls and sloping timbers of mill building	....	....	....	2	....	....	....	2
Cave and fallen rocks	2	....	....	....	....	....	....	2
Pile of lumber and sheet iron in mill building	....	....	....	1	....	....	....	1
House of shingles and scrap in mill building	....	....	....	1	....	....	....	1
Loose rock slabs beneath overhang	....	....	1	....	....	....	....	1
Several boulders	1	....	3	....	1	....	....	5
Under and between two big rock blocks	....	....	1	....	1	....	....	2
Big sandstone block	....	....	....	....	....	1	....	1
Totals	19	1	9	4	3	1	5	42

A locality at which *N. c. orolestes* was abundant and found excellent habitat conditions was three miles north of Almont, 8300 feet elevation. Many rats were trapped alive and released there, and numerous dens were examined. The dens were situated along the front of a cliff-outcrop of the Dakota sandstone part way up the hillside on the east side of the East River Valley. The cliff varied in height from 10 to 20 feet along most of its length and was reduced to low outcrops at the north and south ends where they disappeared into the hillside. The rim of the cliff was formed by a hard reddish layer of cap rock two or three feet thick which protected the softer yellowish sandstone below. As a result of weathering and erosion, the cap rock overhung the cliff at many points, and blocks of it had tumbled down here and there. The cliff front was split up by many vertical clefts and some horizontal crevices resulting from erosion. Above the cliff the cap layer was nearly bare of soil and supported an open stand of blue spruce with fewer ponderosa pines and aspen. Below the cliff were aspens and a few scattered blue spruces and pines. Rose bushes, squaw currant, snowberry, antelope brush, and skunkbush grew among the rocks along the base of the cliff. The soil-covered

TABLE 4.—SHELTER AND TOPOGRAPHY OF N. C. ARIZONAE

SHELTER	Topography and number of dens						
	Cliff above steep slope	Cliff near bottom of gulch	Rimrock outcrop above steep slope	Rocky canyon slope	Rim of steep creek bank	Sandstone hogback	Totals
Vertical cleft in arched sandstone cave	2	....	....	....	....	....	2
Vertical and diagonal crevices	....	1	....	....	....	....	1
Diagonal crevices	....	....	....	....	....	1	1
Vertical and horizontal crevices	1	....	1	....	....	....	2
Projecting outcrop and fallen blocks	....	....	....	....	....	1	1
Big sandstone block	....	....	1	2	1	....	4
Totals	3	1	2	2	1	2	11

slopes farther down from the cliff and above the Dakota sandstone were covered with sagebrush and rabbitbrush. Narrowleaf cottonwoods grew along the river bottom about a hundred feet below the level of the sandstone outcrop.

Toward the south the cliff front was interrupted by a draw cutting through from the east (see Pl. 14, Fig. 1). The outcrop reappeared farther south at the next intersecting draw. Live trapping was done only in the section of cliffs north of the first draw (see Fig. 6).

Three general observations concerning the wood rat dens in this area deserve mention: (1) The distribution of dens was in a linear pattern following the front of the cliff. (2) Virtually every large vertical cleft in the cliff was occupied by a den. (3) All but three of the dens were in such vertical clefts and adjoining crevices. Under these conditions the population limit probably is set by the number of available den shelters.

Wood rat dens were numerous in the cliffs on the west side of the valley of Van Tassel Creek, 32 miles west and 2 miles north of Saguache, 9800 feet elevation, on the Farnsworth ranch. The valley has a flattened-V profile, and most parts of the sloping sides are covered with a kind of bunch grass intermixed with rabbitbrush. On the higher slopes of the west side of the valley there were closed stands of aspen, under which Kinnikinnick (*Arctostaphylos-uva-ursi*), Oregon grape, and scattered grasses were the principal forms of ground cover. Above the aspens was a line of massive cliffs of felsite porphyry, an intrusive igneous rock. The face of the cliff was split up by numerous vertical erosional clefts and some horizontal cracks and was speckled with lenticular pockets or holes up to six inches long, giving the rock a pitted appearance. The lower end of the cliff adjoins the aspen groves and has also many clumps of squaw currant at its base. Farther south and higher up the slope the base of the cliff is more open and grassy with creambush as well as squaw currant abundant. Among the aspens a few yards down the slope are scattered Douglas-firs and blue spruces.

On the east side of the valley the hills and vegetation were different in aspect. The rock outcrops did not form a continuous cliff but a series of rough, broken outcrops. An open forest of bristlecone pine and Douglas-fir covered the hills, with some aspens scattered along the base at the upper edge of the valley slope. Squaw currant, rose bushes, and rabbitbrush were

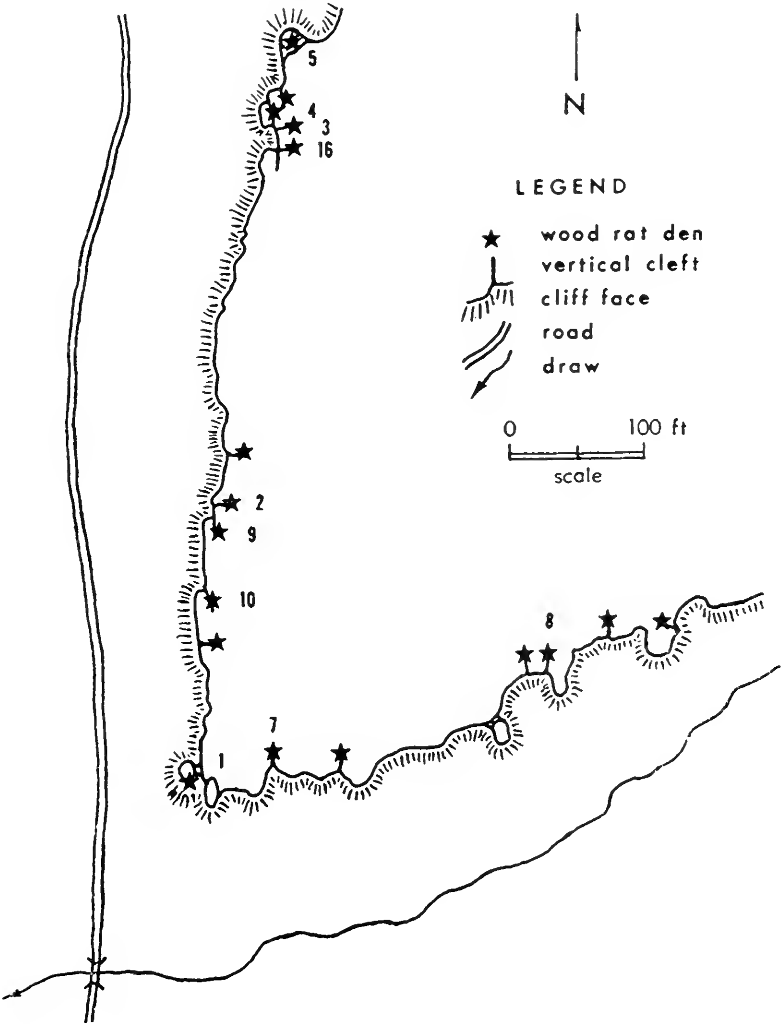


FIG. 6. Distribution of dens three miles north of Almont where a small population of bushy-tailed wood rats was studied. The numbers refer to marked rats and the dens at which they were first live-trapped.

the principal shrubs on the rocky hillside. Near the entrance to the valley there was a small south-facing cliff rising from the valley bottom. The base of the cliff was marshy and had formerly been flooded by beaver activities.

On the west side of the valley there were wood rat dens in nearly all the large vertical clefts in the cliff and under some of the larger fallen blocks and slabs of rock at the base of the cliff. There were long deep middens of rat pellets and old food debris, resembling miniature alluvial cones, coming out of the largest vertical crevices. Some dens were only 10 to 15 feet apart. The number of dens seemed to be limited only by the number of suitable crevices available. There were a few wood rat dens among the rocks on the east side of the valley, but I saw no large middens there. A small amount of wood rat sign and some marmot sign was seen along the small cliff by the valley bottom. Although many excellent dens attested to the suitability of the habitat, the population of wood rats in Van Tassel Valley was at a low ebb in 1948. I saw scarcely any really fresh sign, and a night's trapping yielded only one rat. Remains of two dead rats were picked up at another den.

In the semiarid rolling country of northwestern Colorado a favorable situation for bushy-tailed wood rats was presented by the Fortification Rocks, an igneous dike running in an east-west direction, 16 miles north of Craig. The dominant vegetation was sagebrush and rabbitbrush with scattered gray saltbush and antelope brush. Ten dens were found along the base of the dike. One *N. c. orolestes* was shot in a crevice and four others were trapped. The dike is 6 to 9 feet thick at the base and rises, in places, 20 to 25 feet above the soil on the north side and 40 to 50 feet above the talus rocks on the south side (see Pl. 14, Fig. 2). Viewed from the south, the Fortification Rocks looked like a broken wall with several high sections separated by low sections. Some of the low sections of the wall were interrupted by stretches of the dike so broken down that no wall rose at all above the top of the talus and mantle rock. Wood rat dens were in joints in the base of the dike or in wide horizontal crevices under the base on the south side. None were found among the talus rocks on the south slope.

A locally notorious rattlesnake den was in the largest talus rock pile below the west end of the highest section of the dike. Although the presence of many rattlesnakes (*Crotalus viridis viridis*) in spring and fall may have prevented wood rats from establishing dens in the talus slide, it seems more likely that the wood rats preferred the physical characteristics of shelter provided by the dike itself. Most of the wood rat dens were at the ground level where a few rattlers were also seen. One rattlesnake was seen in a crevice of the dike five feet above the ground level. It seems likely that the wood rats could have found refuge from the rattlesnakes only by climbing high up the dike wall.

On the mountain slopes north of Cement Creek, 3 miles south and 6 to 9 miles east of Crested Butte, between 9000 and 10,000 feet, dens of *orolestes* were examined in various habitat situations. Dens were rather widely scattered because of the relative scarcity of favorable rock shelters. The sequence of rocks forming the principal cliffs and outcrops begins with Pre-Cambrian crystalline rocks near the bottom of the canyon and forming the lower cliffs. Above is a succession of sandstones, mudstones, and quartzite comprising the Sawatch and Yule formations. On the higher mountain slopes above the valley the Leadville limestone forms cliffs and caves. The canyon sides are, for the most part, covered with Douglas-fir forest or mixed Douglas-fir and aspen. Other less extensive types of vegetation are chaparral, grassland, aspen groves, and mixtures of these principal types. Aspens and sagebrush predominate on the valley bottom with fewer conifers. The Pre-Cambrian cliffs have few deep crevices or joints and break down into brittle rocks and fragments too small to afford good shelter for wood rats. Between 300 and 400 yards of cliff frontage and the talus slides below were searched. Only two poor dens were found, at the base of the cliff. A little farther down the valley and higher up the slope the Sawatch formation forms a series of small cliffs or separate rocky points jutting out from the steep canyon side. The rock is composed of many thin layers of sedimentary rocks that break off into a talus of small rocks and slabs. A closed forest of Douglas-fir covers the area, even growing over most of the talus slides. A few widely scattered dens were found in vertical crevices in the Sawatch formation, one of which (480809-1) is described on page 367.

Higher up the mountainside a few small dens were in vertical crevices in a small clifflike outcrop of Yule quartzite and sandstone.

The Leadville limestone provides more suitable shelters for wood rats than the underlying formations. Several dens were seen in limestone cliffs and caves high on the north slope of a gulch opening into the lower end of Cement Creek valley from the north. A few other dens were in isolated limestone outcrops on the west side of the gulch and near its mouth. The most prominent dens were in two large caves and associated crevices. A long vertical crevice in the limestone cliff west of the caves also sheltered a den. Another was in a small cave and horizontal cleft screened by a thicket of chokecherry bushes on the west slope. The vegetation of the gulch bottom and lower slopes was mixed Douglas-fir and aspen. Higher up on the west side of the gulch the trees gave way to low chaparral composed mainly of serviceberry, snowberry, and sagebrush. Below the limestone outcrops were thickets of chokecherry and serviceberry. On the upper northeast side of the gulch scattered aspen and second growth Douglas-fir gave way to a low chaparral of creambush and snowberry with scattered squaw currant, serviceberry, and sagebrush. Along the base of the cliff was a tall thicket of creambush and clumps of squaw currant. Wood rat dens were associated with each of these plant communities. The wood rats found ample cover and abundant food in all of them. The only prominent plants of low palatability were creambush and sagebrush.

In Rabbit Canyon, 20 miles west and 3 miles north of Saguache, 9000 feet elevation, at or near the type locality of *N. c. orolestes*, there is a low rimrock on the north side of the valley dipping eastward down the valley. The rim outcrop is of volcanic rock, a vitrophyre, that provides shelter for wood rats in crevices and under fallen blocks. Numerous dens were seen, and it was noted that loose blocks and boulders below the rim were more frequently used here than at three miles north of Almont, perhaps because of the scarcity of good vertical crevices in Rabbit Canyon. There were a few scattered pines (*P. ponderosa* and *P. aristata*) and Douglas-firs on the north side of the valley and a fairly open forest of the same trees on the south side (north-facing slope). The principal shrubs scattered among the rocks below the rim were squaw currant, skunkbush, and soapweed. Sparse grasses and bare soil covered the lower slope. The vegetation was a rather odd mixture of species that probably can best be called upper Transition Life-zone. The occurrence of soapweed was unusually high for this plant, which is ordinarily characteristic of the Upper Sonoran Life-zone and owes its survival in Rabbit Canyon to the favorable, sunny dry exposure of the south-facing slope.

The north rim of Cahone Canyon southwest of Cahone provides excellent habitat for wood rats. The rim and upper slopes of the canyon were formed by the Dakota sandstone. The lower slopes were formed by variegated shales and sands of the Morrison formation. The rimrock varied in height, in some places being only a low outcrop, in others forming low cliffs 25 or more feet high. The sandstone rim was broken up by numerous vertical crevices, and undercut in places by weathered horizontal clefts (see Pl. 12, Fig. 1). Dens were abundant under fallen blocks as well as in crevices in the standing rimrock. The top of the mesa or upland was heavily wooded with large piñons and junipers, except for areas to the north and east that had been cleared for cultivation of pinto beans. Piñons and junipers were the dominant plants on the canyon sides as well as the upland. Typical shrubs and forbs were serviceberry, mountain-mahogany, antelope brush, Mormon tea, snakeweed, *Penstemon bridgesii*, and *Lepidium montanum*. Hunger cactus and bunchball cactus were also numerous. The floor of the canyon was covered with sagebrush and had little, if any, cactus.

Although wood rat dens were abundant along the rim of Cahone Canyon and among rocks on the steep slope, no dens were seen on the canyon bottom, probably because of the scarcity of sandstone blocks and suitable outcrops. Two kinds of rats were trapped in nearly equal numbers, *N. cinerea arizonae* and *N. mexicana inopinata*. Although it was not always possible to distinguish the dens of the two species without trapping the occupants, a few average differences between the dens were usually evident. The larger vertical crevices and clefts in the rimrock and the larger fallen blocks usually sheltered the bushy-tailed wood rats whereas the smaller, usually horizontal crevices and smaller fallen blocks usually sheltered the Mexican wood rats. Also, the bushy-tailed wood rats usually accumulated about their dens larger amounts of sticks and bones, often of larger size than the pieces collected by the Mexican wood rats.

In Dolores Canyon near Gateway there seems to be a fairly distinct habitat separation between *N. c. arizonae* and *N. m. inopinata*, as described on page 450.

The habitat of *N. c. rupicola* in northeastern Colorado is confined to the rim of the High Plains north of the South Platte River. The rim is marked by a line of south-facing bluffs and detached buttes north of which extends the undulating upland plain. South of the bluffs extends the broad gently-sloping valley of the South Platte River which has been eroded several hundred feet below the former surface of the Tertiary mantle, of which the High Plains rim is a remnant. The rim of the bluffs is a coarse, light gray sandstone (see Pl. 14, Fig. 3), which provides den shelters for *rupicola* in vertical and horizontal crevices, in small caves, and under large fallen blocks of rimrock. North of Stoneham where dens of *rupicola* were examined the vegetation of the upland was grazed short grass, hunger cactus, and soapweed. On the steep rocky slope below the rim, shrubs were dominant, most abundant of which were chokecherry, skunkbush, and golden currant. Rabbitbrush and squaw currant were less abundant. There were a few stunted, half-dead western hackberry trees.

DENS

The bushy-tailed wood rat prefers vertical crevices in high cliffs but occupies a variety of other shelters where high vertical crevices are absent or too few for the existing population. Dens in cliffs are situated also in horizontal crevices and ledges, those higher up being preferred to those at the base of the cliff. Many sticks and bones commonly are carried into the den crevice. They partly close clefts that are too wide for best protection of the rat, and occasionally support feeding platforms or nests in vertical clefts that lack horizontal crevices or shelves. *Neotoma cinerea* has a moderately strong collecting instinct and nearly always accumulates much material at the base of its den even when the objects are of no advantage.

Large caves also are much used by *cinerea.* Nests and resting places ordinarily are high above the floor, in crevices, on small ledges or on projections of the ceiling or walls. In fairly dark caves the nests usually are cup-shaped and exposed to view from the interior of the cave. Such exposure of the nest is probably because the interior of the cave, for the rat, has conditions resembling those of the interior of a den in a large cleft. Walls of caves that have long been occupied by wood rats contain large black or dark brown deposits of feces and urine on projections and ledges used as lookout perches or resting places. Below such perches the deposits extend usually far down the walls as a glossy blackish varnish grading into a dull dark stain. Some walls are almost solidly coated with these deposits (see Pl. 17, Figs. 3 and 4).

When natural cliffs and caves are absent, abandoned mine shafts, ore mills, cabins and other kinds of buildings are occupied. In the physical characteristics that they provide for the protection and activities of wood rats, these man-made structures differ little from caves. Mines, buildings, and caves all have wide expanses of vertical walls, high ledges or timbers, and roofs or ceilings sheltering large living spaces. These conditions provide refuge from ground predators, support for nests, space for food stores, and resting places inaccessible to most enemies. That the wood rats often feel secure in such interiors is indicated by the frequent use of inner nests exposed to view within such caves or buildings. To the rat, the entire cave or room is the den, corresponding to a large stick house of *N. floridana* or *N. fuscipes.* But, if the cave or room is too large or too bare or too open, the resident rat usually makes use of some additional smaller shelter within the cave or building, such as crevices, space between double walls, or piles of lumber or trash within which it places its nest. Use of crevices within large caves is also an indication of the superiority of vertical crevices over caves and buildings as choice den shelters. Extensive and high crevices in a cliff offer all the advantages of a cave with the additional one of protection against the entry of large animals.

Some of the less choice kinds of shelter sometimes used by this species are deep horizontal or diagonal crevices in low cliffs or rock outcrops, ledges or spaces on the ground level under the bases of outcrops, clefts between large detached blocks of rock, irregular spaces among boulders or talus rocks, and the space on the ground beneath a large block of rock. If any of these shelters occur under an overhanging cliff or an overhanging ledge the situation is much more attractive to *cinerea.* Under large overhangs nests are often exposed to view, as they commonly are in caves.

N. cinerea often accumulates a pile of sticks, bones, and other debris large enough to form a house, but this trash nearly always is piled in the base of a wide vertical cleft or between blocks of fallen rock where the trash closes or restricts openings into the rock den. Such a pile has no inner passages or structure. Beneath many dens that are unusually secure, the accumulated sticks probably serve no useful purpose and merely result from an instinctive behavior pattern. Under rare circumstances a rat will build an actual house with one or more chambers and passages and containing a nest. Grinnell, Dixon, and Linsdale (1930: 517-520) described stick houses made by *N. c. alticola* in the branches of juniper trees in northeastern California. These houses usually were associated with hollow tree trunks, which served as dens not unlike vertical rock crevices.

Although in this study I saw no dens of *cinerea* away from rock shelter or some building of man, dens were found by Merrit Cary (1911: 111) in other situations in the rough country bordering the lower Snake and Bear rivers. In that region he found the preferred dens to be in hollow junipers. Other dens were in rocky bluffs, adobe banks of arroyos, hollow cottonwoods, and occasionally in thickets of buffalo berry (*Shepherdia*).

Large sticks and bones are more abundantly used as den materials by *N. cinerea* than anything else. Sticks are gathered from whatever kinds of trees and shrubs are available. Bones of deer and rabbits greatly outnumber all other kinds, but those of a great variety of large and small mammals and birds are likely to be found mixed with the sticks.

TABLE 5.—MATERIALS ACCUMULATED AT DENS OF N. CINEREA

MATERIALS	Number of dens			
	N. c. orolestes	*N. c. arizonae*	*N. c. rupicola*	Totals
sticks	41	10	3	54
sagebrush	16	1		
Douglas-fir	7			
Ribes	6			
aspen	5			
juniper	4			
pine	3	1		
sawed wood	4			
chokecherry	2			
skunkbush	2			
antelope brush	2			
shingles	2			
saltbush		2		
cottonwood	1			
driftwood	1			
mountain-mahogany		1		
unidentified	13	7	3	
bones	33	7	2	42
rabbit	13	3		
deer	13	1		
stones	11	4	2	17
cones	8	2		10
Douglas-fir	6			
ponderosa pine	3			
bristlecone pine	2			
piñon		2		
limber pine	1			
blue spruce	1			
cactus joints	5	3	1	9
Opuntia polyacantha	5	3	1	
O. davisii		1		
livestock dung	5	2		7
small branches and twigs	3	2	1	6
bark	4	1		5
Douglas-fir	2			
ponderosa pine	2			
juniper		1		
grass	4			4
broken glass	4			4
owl pellets and debris	3			3
nails	3			3
burlap	3			3
tarpaper	3			3
paper	2	1		3
dry weed stalks			3	3
thistle stalks and heads	2			2
chunks of rotten wood	2			2
feather	2			2
dry rabbit foot	2			2
cotton cloth	2			2

TABLE 5.—*Concluded*

MATERIALS	Number of dens			
	N. c. orolestes	*N. c. arizonae*	*N. c. rupicola*	Totals
cardboard	2			2
carnivore scats	1	1		2
yucca blades, stalks and capsules	1	1		2
tufts of moss	1	1		2
potsherds	1	1		2

Each of the following items was present at one den of the subspecies: *orolestes:* mummified chipmunk, deer hair, dry rattlesnake carcass, shed rattlesnake skin, peach pit, pieces of rope, pieces of leather glove, shotgun shell, coal, bolt, nut, hacksaw blade, wire, porcelain insulators; *arizonae:* roots, charred wood, porcupine quills.

Nests of the bushy-tailed wood rat are usually cup-shaped, but occasionally the nest is roofed over, being domed or ball-shaped. A few ball-shaped nests were located in an old mill under piles of shingles and other trash comparable to stick houses. Most nests are situated in narrow crevices or on well sheltered rock shelves more than ten feet above ground. Such sites ordinarily are so dry and well protected against inclement weather that the occupants probably feel little need for a domed roof on the nest. Nests high up on the walls of caves, or on timbers of abandoned buildings having intact roofs and walls, ordinarily are cup-shaped. The materials of the nest are more or less loosely placed together, not at all interwoven as in a bird nest.

Nests are made of a variety of fibrous materials, according to the resources available. Nesting materials used were shredded sagebrush bark, shredded juniper bark, dry grass, yucca fibers, and fibers produced by man. Shredded bark of sagebrush is the material most commonly used by *N. c. orolestes* between 7000 and 10,000 feet elevation, because of the abundance of sagebrush and relative scarcity of junipers there. Below 7000 feet, in the piñon-juniper association, juniper bark seems to be used by *arizonae* as much or more than sagebrush. Grass is less frequently used, usually when neither sagebrush nor juniper is close at hand. Yucca fibers are used by *rupicola* out on the rim of the High Plains, where grass seems to be the only other suitable material available. Nests in the abandoned buildings of an old gold mill were made of wads of waste cotton, jute oakum, and hemp. Other materials sometimes mixed with the principal fibers in trivial amounts are string, bits of chewed cloth, deer hair, feathers, moss, and flower cuttings of rabbitbrush.

From the 58 dens of *cinerea* studied, a total of 37 nests was obtained. These 37 were taken from only 19 dens, whereas at the other 39 dens no nest was accessible. Three of the dens yielded 4 nests each, 2 dens yielded 3 nests, and 5 dens yielded 2 nests each. A single nest was found at each of the 9 remaining dens. The proportion of dens having multiple nests is probably higher than shown by these figures because of the large number of nests that were inaccessible.

A clearer picture of the shelter requirements and denning behavior of the bushy-tailed wood rat can be conveyed by description of a few of the 57 dens of this species that were studied comprehensively. The following examples have been selected to illustrate the considerable variety of shelter situations that fulfilled the needs of this wood rat, and the various ways in which individual rats made use of the available resources of the environment.

A den 21½ miles west and 4½ miles north of Saguache was nearly ideal for the bushy-tailed wood rat. An outcrop of extrusive igneous rock formed a southwest-facing cliff broken by many nearly vertical joints. Between two such joints seven feet apart a cuboid block had dropped away from the base of the cliff leaving an overhanging block sheltering the walls of the "room" below. Projections on the walls under the overhang had been used as perches by the wood rats and were coated with black fecal deposits. On the walls below the crevices and lookout perches there were black shiny stains. The long narrow crevices on each side of the overhang extended all the way to the top of the cliff and were the principal living space used by the rat. They may have been connected by another vertical crevice across the back.

The dry rocky mountainside supported an open forest of ponderosa pine, Douglas-fir, blue spruce, and aspen. Mixed shrubs were dominant in the open areas, including squaw currant, gooseberry, wild raspberry, rabbitbrush, rose, and shrubby cinquefoil. Food litter consisting primarily of twigs of rose and squaw currant, with considerable Douglas-fir and pine needles, had accumulated on the ground under the north crevice. There were also food litter and sticks high up in the crevice, which was four and a half inches wide at the bottom edge and narrower above. Other materials on the midden below the crevice were deer bones and an old cone of the limber pine. A grass nest was wedged in the overhead crevice four feet above the overhang. A subadult male (490728-5) was caught at this den.

A typical den of *N. c. orolestes* was in a large vertical cleft in the face of a cliff 3 miles south and 6½ miles east of Crested Butte. A subadult male (480809-1) was trapped at this den on 9 August 1948. The cliff was formed of broken jagged bands of interbedded sandstone and mudstone. The rocky talus slope below the cliff supported a stand of Douglas-firs with scattered blue spruce. A dead conifer had fallen over against the cliff with its top lodged in the upper part of the vertical crevice. An account of the habitats in the vicinity of this and the two next described dens is given on pages 360 and 361.

Large numbers of Douglas-fir sticks and large bones had been carried into the vertical cleft at three successive levels and served as platforms as well as protection against the entry of larger predators. On the highest layer of sticks there was a bed of Douglas-fir needle cuttings three inches deep. The middle level also had many needle cuttings. There was much grass on the bottom level of sticks and bones. Although only deer bones were large and numerous enough to add much to the structure, bones of several kinds of smaller mammals were among the sticks and litter. Other small items were owl pellets, feathers of a great horned owl and a magpie, and a piece of leather. An owl roost in the upper part of the same vertical crevice was the source of much of the material.

Higher up the mountainside and perhaps a quarter of a mile farther west a south-facing limestone cliff of the Leadville formation contained a long narrow vertical crevice that extended from the base to the top of the cliff, estimated to be 50 feet high. Although this crevice contained only a little debris, a subadult female (480810-4) was trapped in the base of the crevice. There were no sticks or stored foods visible in the crevice above the ground level, but a few sticks and a small pile of cuttings were under and beside a three-foot slab of rock leaning against the cliff five feet east of the crevice. The only bones present were the dentary and pelvis of a marmot. Most of the sheltered living space used by this rat probably was high up in the crevice far out of my reach.

Another den was in a horizontal crevice and small cave in a less prominent exposure of the same limestone formation. The narrow crevice, in some places no more than a groove, followed a bedding plane several feet above the base of the outcrop. The bedding plane also formed the floor of the cave, which was a tunnel one to two feet high running parallel to the face of the cliff and opening to the outside through four holes along the crevice. A chokecherry bush screened the cave entrance which was most used by the wood rat. A deep bed of shrub sticks up to three quarters of an inch in diameter lay inside the mouth of the cave. Three bones were among the sticks, which were mostly of chokecherry. A bed of foliage cuttings three to four inches deep in the cave was composed mostly of chokecherry, snowberry, and figwort, with a variety of other cuttings less numerous. Branches of chokecherry and creambush growing at the base of the outcrop had both been heavily pruned. The den had a neat orderly appearance and ample interior space. A large adult male wood rat (480810-2) was trapped there. Marmot feces were seen around the den, probably resulting from previous occupancy of some part of the cave tunnel by a marmot.

A den of poor quality because of the dampness was in a large limestone cave a mile east and seven miles north of Hermosa at 8100 feet elevation. The mouth of the cave was 30 feet wide and 15 feet high and overlooked a steep valley slope facing south. The cave was between 100 and 150 yards in length, extending nearly straight into the mountainside. The den was 125 feet in from the mouth on top of a block of limestone that had fallen from the roof, and under a second block leaning on the first. A subadult male rat (490912-1) was trapped there on 12 September 1949.

Below the mouth of the cave there was a dense stand of scrub oaks. A closed forest of ponderosa pines and Douglas-firs grew on the slope below and the nearly flat upland bench above the roof of the cave. Other trees and shrubs growing in the vicinity of the cave entrance were limber pine, Rocky Mountain juniper, serviceberry, and rose.

The ceiling of the cave was flat and nearly level. The floor rose from the entrance to the top of a low transverse ridge of rock waste and dropped down about 5 or 6 feet to the bottom of the large dimly lighted section in which the den was situated. From there on back, the floor rose toward the roof and the sides converged as the cave became smaller. Water dripping from the ceiling and seeping down the walls kept the interior damp and had in the past formed a series of terrace-like pools descending through the rear two thirds of the cave toward the mouth. Most of the pools had since dried up, and only a few shallow pools remained.

There were many bones of various sizes on the two boulders associated with the den and on the floor of the cave. The bones, in fact, outnumbered the sticks. Probably this was because most of the bones were of animals that either died in the cave or were brought in by predators, whereas the rats themselves had to bring the sticks all the way in from the mouth of the cave. The bones included parts of 1 bear, 1 badger, 1 domestic cat, 3 deer, 2 sheep, 1 cow, 2 porcupines, 1 Canada goose, 1 dusky grouse, 1 pocket gopher, and 4 wood rats. Other materials accumulated about the den were many small stones, a few pieces of broken bottles, a potsherd, a few cones of ponderosa pine and Douglas-fir, and a mummified chipmunk. On top of the main block and behind the leaning block was a nest composed of moss, deer hair, and juniper bark. There was a supply of food stored on a ledge running across the ceiling above the ridge on the floor of the cave. The store contained 88 mushrooms partly dried but damp and decomposing inside and some cuttings of *Smilacina* partly dry but mildewed. Food litter about the den consisted of a wide variety of shrub twigs and shrub and forb cuttings, none in large amount.

An excellent den three miles north of Almont was unusual in having four nests exposed to view from the base of the cleft in which the den was situated. A young adult male (480720-5) was trapped there on 20 July 1948. The habitat is described on pages 357 and 358. The den was in the upper part of a vertical erosional cleft in a low south-facing cliff of Dakota sandstone. Good shelter was provided by a long overhanging ceiling of caprock. The east wall of the cleft projected 15 to 20 feet south to the front of the caprock, from which point the cliff front extended east with no overhanging rim. In other words the overhanging caprock bridged a recession in the cliff line where a section of cliff west of the cleft had dropped away. The height of the cleft was approximately 15 feet from the ceiling to the base of the cliff. The cleft was two to three feet wide at the base, narrowing upward to the ceiling, through which it continued only as a crack hardly wide enough for a wood rat. The length of overhang was 15 feet on the east side and 10 feet on the west side of the den. Under the ceiling on the east side of the cleft there was a horizontal crevice where the bedding plane under the caprock had weathered out. This crevice was a foot wide at the front but decreased to 2 or 3 inches wide at the back of the den. A similar but smaller crevice extended west of the vertical cleft. There were at least 10 points on the east wall beneath the overhang and 5 points on the west wall that were used as lookout perches or resting places, as indicated by the black solid fecal deposits on the perches and blackish stains on the wall below.

A half dead bush of squaw currant grew out of the cleft five feet above the base. A midden of fecal pellets and some food litter lay in the cleft immediately above the squaw currant and on the ground at the base of the cleft. A moderate number of sticks, mostly of sagebrush, were scattered in the vertical cleft and the horizontal crevices on each side. There were also numerous bones, including a marten skull, the femur of a beaver, leg bones of rabbits and deer, and a mandible of a great horned owl. On the ground below the den cleft there was weathered debris from owl pellets containing remains of *Neotoma* and *Thomomys*. A cliff swallow nest in service was hanging from the underside of the overhanging caprock 3 or 4 feet from the rim of the horizontal crevice above the eastern wall.

All four nests were open on top and cup-shaped. They were approximately nine inches in outside diameter and four inches across the inside depression, which was about an inch deep. Nest No. 1 was in a rock recess on the west wall of the cleft and was composed mostly of shredded bark of sagebrush, as were the other nests also. On the underside there were dry flower cuttings of rabbitbrush, and on the side and rim of the nest there were some coarse blades of rye grass (*Elymus*). Around the outside of the nest there were many fresh food cuttings, a mandible of *Lepus*, and a mandible of *Sylvilagus*.

Nest No. 2 was on a thin slab shelf below the celing and directly over the back of the vertical cleft. There was barely enough space above the nest for the rat to crawl in and out. A few recent cuttings of rose and rabbitbrush were in the nest. Behind the nest a skull of *Sylvilagus* and an owl pellet were wedged between the thin rock slab and the ceiling. An owl could not conceivably have deposited its pellet in such a position.

Nest No. 3 was on the shelf overlooking the east wall of the cleft where the horizontal crevice under the ceiling was at least a foot high. This position commanded a good view out of the den and across the gulch while being at the same time well sheltered by the caprock. On the front side of the nest was a piece of soft cotton flannel having an area of about 40 square inches. Food cuttings lay on the ledge around the nest. This nest, like the two preceding, was in good repair, and apparently in current service.

Nest No. 4 was on the same shelf but roughly six feet farther south at the front of the cleft and beside a vertical piece of the rock wall that partly shut the nest off from the outside. Nest No. 4 was old and partly disintegrated, with its bark shreds finer and crumbling to powder. The inner (north) side of the nest had fallen down flat. No cuttings were present on or near this nest which was obviously in disuse.

Not far from the preceding den the same cliff had a deep narrow cave with an old wood rat den and heavily stained walls (see Pl. 17, Fig. 3). A thicket of chokecherry bushes partly hid the mouth of the cave, which was large enough for a person to walk into with ease. The ceiling was 6 to 8 feet high near the entrance. The walls gradually converged toward the rear end of the cave which was perhaps 25 feet in from the mouth. The cave floor was dry and sloped downward toward the outside.

Most of the east wall of the cave was stained and streaked with black fecal and urinary deposits below the many projections and narrow ledges in several rows along the wall from the ceiling nearly to the floor. The opposite wall was almost sheer and had only a few perches and fecal stains. Innumerable generations of wood rats must have inhabited the cave in order to accumulate such quantities of fecal deposit.

In the rear portion of the cave there was a pile of sticks between the two walls, which were at that point no more than two feet apart. On 27 July 1948 when I watched a wood rat moving about in the back of the cave, the stick pile was approximately a foot high. When I returned on 15 September 1948 the appearance of the den had changed greatly. Much new material had been added to the pile, raising it to a height of 27 inches at the front, with an estimated volume of more than two bushels of sticks. On top of the pile and behind it there was a deep bed of green dry food cuttings, most of it lying behind the sticks. The bed of stored cuttings was estimated to amount to half a bushel, consisting of equal parts *Chrysothamnus greenei* and chokecherry.

Three exposed cup-shaped nests were visible from within the cave on 15 September. One nest was in a niche between the top of the east wall and the ceiling, almost directly above the side of the stick pile. A new nest not present on 27 July lay behind the stick pile. Far in the rear of the cave, where the walls converged to a small tunnel, a third nest lay on the elevated floor of the cave. A wood rat was observed in this nest on 15 September.

A good den, though small, was in narrow crevices under an overhanging limestone outcrop of the Hermosa formation six and a half miles southwest of Silverton, 10,000 feet elevation. The outcrop had a western exposure overlooking the steep mountainside above West Lime Creek. The den was in a crevice on a ledge dipping to the northeast immediately under the overhang. The crevice seemed to have resulted from the weathering of an interbedded layer of shale three feet above the base of the limestone. The three foot thickness of limestone below the ledge was partly broken into flagstones separated by narrow crevices, some of which were utilized by the wood rat, an adult male (490719-9), trapped at this den on 19 July 1949.

The ledge line beneath the overhang could be recognized for a long distance along both sides of the V-shaped valley and seemed to provide the only shelter crevices deep enough for *N. cinerea*. The outcrop was not broken by any sizable vertical crevices. Along a quarter mile section of the outcrop four dens were found at the same horizon in the limestone.

Montane grassland covered the canyon side, and scattered timber grew mostly along the bottom. A clump of willow stood in front of the den. On a bench above the outcrop there were a few aspens. Three kinds of *Ribes*, rose, snowberry, and swamp honeysuckle grew along the base of the outcrop. Materials gathered on the ledge supporting the den included sticks up to 15 inches long and 2 inches thick, a few stones, two marmot bones, and a long gnawed feather. There were many green cuttings of eight species of forbs, as well as twigs of aspen and *Ribes*. In dark corners of the shelf far back under the overhang there were two shallow cup-shaped nests made of soft dry grass. One measured nine inches in outside diameter and three inches thick from the outside to the edge of the pocket.

A large den at the base of a cliff one mile southwest of Almont was unusual in that shelter was provided by a conical pile of talus blocks filling a notch in the cliff front. The cliff was of biotite granite and gneiss which broke up along irregular joints. In the cliff close to the talus rocks there was no vertical cleft comparable to those in the sandstone occupied by wood rats north of Almont. The talus cone was roughly 50 feet long. The largest block, much larger than the others, was 12 feet long and lay below the smaller rocks under which most den material and food were found. A subadult male (490722-1) was caught there under rocks close to the cliff wall.

On the face of the cliff between 6 and 10 feet above the ground at the south edge of the talus pile there were more than six fecal perches on narrow projections and irregularities jutting from the rock wall (see Pl. 16, Fig. 1). Within the pile of talus there were also a few fecal perches on the points and upper angles of rocks under cover of other rocks. The fecal deposits on all these perches differed from the usual deposits seen on the walls of caves in that these were small irregular consolidated piles without the dark glossy glaze and stain running down the wall below the perch. The difference is almost certainly due to exposure to weather. On this wall there is no roof or overhang, and rain washes down the urine and dissolved fecal material before it hardens. Perches exposed to the sky such as these are rarely seen. It is difficult to see how a rat using such an exposed wall can avoid being picked off by an owl. Possibly that has been the fate of previous occupants of this den.

Den materials under the rocks consisted mostly of sticks of chokecherry, with some of sagebrush and squaw currant; but the total amount of sticks was not large. There were some deer bones that had been brought from a skeleton lying at the base of the cliff a few feet south of the talus rocks.

A dense clump of chokecherry grew against the cliff at the head of the talus cone. The clump had been heavily pruned, and its twigs were the most abundant food litter. Dogwood and serviceberry bushes near the den had also been pruned, to a lesser extent. An old storage supply amounting to five gallons under and between rocks consisted of dry, mostly green leaf cuttings of chokecherry. All the leaves exposed on the surface of the pile had turned brown. The storage probably dated from the previous autumn.

A den in Rabbit Canyon, 20 miles west and 3 miles north of Saguache, was among boulders of volcanic rock on a moderate southeast-facing slope. The den was large and extended under and between many boulders up to 7 or 8 feet in length. It had six middens and entrances on the sandy soil between various boulders. A subadult female (480801-1) was obtained at this den on 1 August 1948. For a description of the habitat see page 361.

A Douglas-fir tree stood 50 feet from the den. On the ridge farther away stood a bristlecone pine and a few ponderosa pines. There was a considerable quantity of den materials scattered under the rocks, including sticks of pine and squaw currant, bark and cones of ponderosa pine, twigs and one cone of bristlecone pine, Douglas-fir cones, dry blades and stalks of *Yucca glauca,* and bones (coyote, sheep, horse, cottontail, prairie dog, badger, and bird).

A huge block of sandstone resting at the edge of the Navajo River bottom sheltered a den at which an adult male (491116-2) was trapped on 16 November 1949. The most accessible part of the den with most debris was under a corner of the block held three feet off the ground where the foot of the hill met the valley bottom. Although most of the other sides of the block were solidly embedded in the soil the den probably extended under a large part of the rock either in narrow spaces or in tunnels between rock and soil. A second entrance to the den was on the upper side of the slope in a small cleft between the main block and a detached fragment. The length of the block was 50 feet (paced) and the height 20 to 25 feet (estimated).

Narrowleaf cottonwoods, willow, Rocky Mountain juniper, and alder grew on the bottomland close to the den. On the valley sides the dominant vegetation was scrub oak with scattered ponderosa pines and Douglas-fir. Sticks of driftwood, cottonwood, and other kinds were scattered under the elevated corner of the block, but twigs and fallen leaves covered most of the soil there. One cone each of pine and Douglas-fir must have been brought from more than 50 yards away. Food litter consisted mainly of twigs of cottonwood and willow and fresh cuttings of sweet clover.

A den two miles north of Ridgway was in a long narrow horizontal crevice approximately ten feet high on a cliff (see Pl. 18, Fig. 1). The den was in fair condition, tidy, but with scanty sheltered space. The cliff was formed of a rather thinly bedded series of sandstone, shale, and gypsum beds. The occupied crevice, 2 to 5 inches high and 3 to 15 inches deep, was in the weathered bedding plane on top of a red shaly bed and immediately below a projecting layer of hard sandstone. A young adult male (491101-1) was trapped at this den on 1 November 1949.

The cliff stood at the head of a gulch and against the foot of a steep slope wooded with piñons and junipers. Common shrubs along the cliff base were serviceberry, scrub oak, mountain-mahogany, Mormon tea, rabbitbrush and sagebrush. Parts of the crevice were walled in at the front with sticks and a few small bones. Elsewhere along the shelf the material consisted mostly of shredded juniper bark (old nesting material) and a few dry joints of prickly pear. Food litter consisted mainly of cactus spines, juniper cuttings, and the leaves and seed plumes of mountain-mahogany. An old cup-shaped nest was far back in the crevice. Some food litter and fecal pellets were scattered on the ground below the crevice.

Another den in a horizontal crevice, 16 miles north of Craig, was improved by partial closure of the front with a barricade of den materials. This den was at the ground level under the base of an igneous dike known as Fortification Rocks. The steep slope below was strewn with talus in use as a rattlesnake den. The topography and vegetation are described on page 360. At this den I caught the largest wood rat known to me from Colorado, a male *orolestes* (480903-4), 425 mm in length and weighing 427 grams.

The den-crevice was roughly 18 inches high at the front and ran far back under the dike beyond reach. A large amount of sticks and other materials were accumulated in the crevice, especially toward the front where they were heaped up to a depth of a foot in places, thus forming a barricade almost closing off the interior of the crevice. This structure greatly increased the protection against predatory mammals and birds, but was of no value against rattlesnakes, of course. Presence of rat pellets under rocks on the talus slope indicated that the wood rats even frequented the same rocks most used by rattlers.

Den materials were mostly sticks of sagebrush, with bones, prickly pear joints, cow dung, a thistle, a dried rattlesnake carcass, and a shed skin of a rattler. Food cuttings and litter in the den were mainly of rabbitbrush, lupine, and *Astragalus*. Approximately a bushel of cuttings filled a back chamber of the crevice. A nest of shredded sagebrush bark lay just in front of the storage pile.

At a den in the same dike, some distance east of the rattlesnake den, a wall of sticks had been extended by a barricade of stones 1 to 3 inches in diameter. The den thus partly enclosed was at the west end of a large deep horizontal crevice 6 to 8 feet above the base of the dike. The west end of the cleft had been closed in front by sticks piled up from the shelf to the ceiling, a height of roughly 12 inches. A few stones were interspersed with the sticks. From the east end of the stick wall the barricade of stones extended two feet farther along the shelf. The pile of stones, which was a foot wide and up to six inches deep, formed a partial barrier that appreciably reduced the exposure of the open side of the chamber behind the stick wall. Although no wood rat was obtained or seen at this den, the identity of the occupant as *cinerea* is almost certain, because no other species is known to occur within 75 miles of Fortification Rocks.

All of the foregoing examples of dens have been in naturally occurring kinds of shelter present long before the arrival of man. At the Gold King Mill north of Hesperus many dens were seen in the old abandoned mill and outlying buildings, showing some of the ways in which *N. c. orolestes* uses man-made structures and materials as substitutes for analogous kinds of "natural" shelter. The habitat was a southwest-facing mountainside with aspen and grassland in the cleared area around the mill and montane coniferous forest outside the disturbed area.

A den high on the wall of an old ore bin was in a situation comparable to that inside a fairly open cave or under a large overhang. There was much debris and food litter on 4 by 8 inch beams supporting the outer siding and the remaining part of the inner wall of the bin. (See Pl. 19, Fig. 1). Two nests were on separate beams, in the crevicelike spaces between the wall boards. One of the nests was on the far end of its beam behind a pile of sticks. Both nests were made of cotton, jute and hemp fibers, string, and wads of tow.

Den materials used to obstruct the "crevices" in the wall and scattered on the exposed beams included sticks of sawed wood and shingles mostly, stones up to 3¼ inches long, 3 dry snowshoe hares' feet, porcupine bones, a chicken breastbone, tarpaper, paper, nails, nut, bolt, broken glass, cotton rag, and burlap. Approximately two gallons of assorted food cuttings were under sticks in the wall. On 5 July 1949 a lactating female (490705-1) was trapped at this den.

A large, long-used den was on the floor above the ore bins. A large amount of sticks and assorted debris had been piled in the corner of the room in a narrow triangular space between the two walls and heavy timbers on the floor. The walls and the floor above were fairly tight and kept the stick house dry, except for what little rain might blow in through a doorway in the southwest wall. The stick pile was 25 inches high and spread out at the base to cover most of the triangular floor space measuring 11½ feet on one wall and 3½ feet on the other. A lactating female (490705-3) was trapped at the den on 5 July 1949 and a nearly grown young was seen in the stick pile.

The house was built mostly of split shingles with a large assortment of other trash contributing. These included scraps of sawed lumber, bones, stones, carnivore scats, lumps of coal, nails, glass, pieces of leather glove, tarpaper, cardboard, burlap sack, pieces of rope, wire, and porcelain insulators. A large domed nest was under a bent piece of sheet iron in the back corner of the house. Beside the nest was a pile of aspen twigs with all the bark eaten off. The nest (see Pl. 20, Fig. 1) measured 12 inches long, 12 inches wide, and 7½ inches high. The pocket was 4 inches deep and the opening 3 by 3½ inches. A second nest was at the opposite end of the stick pile under boards and rags. It was smaller than the first and probably was domed but was crushed in by sticks in dismantling the den. Both nests were made of cotton wadding, jute, tow, hemp rope fibers, and string.

The den was not confined to the space under cover of sticks and trash. Horizontal beams and stringers supporting the joists overhead were commonly used as feeding and resting places, as indicated by the abundance of pellets and food litter on them and the many dark stains running down the walls. There were also two open, cup-shaped nests on the 10 inch stringer against the wall and supporting the ends of the joists above the house. Both these nests appeared to be in service. A shallow dilapidated cup-shaped nest lay on the floor in the corner 15 feet southeast of the stick pile and behind timbers and planks. This nest was probably out of service but may once have belonged to the same den.

Another den in the old gold mill was under a big pile of sawed timbers, planks and corrugated sheet iron in the corner of another room. This pile of objects too large for the rat to move provided ample sheltered spaces, and only a little trash had been gathered by the rat to add to it. Two outlying buildings contained nests exposed to view on high beams, a nest in the bottom of a stove pipe where it bent to pass through a wall, and a nest on the grate inside an assay furnace.

An old and excellent den of *N. c. arizonae* was in a large vertical cleft through the roof of a wide, arched sandstone cave 10 miles west and 5 miles north of Rangely. This was one of two caves undercutting a south-facing sandstone cliff so as to leave broadly arched cave roofs on the rim of a gulch. The cave mouths were perhaps 75 to 100 feet wide, a third as high in the middle front, and half as deep.

Each cave had a vertical cleft cutting through the roof parallel to the cliff front and about half way between the front and rear of the cave. In these clefts, which penetrate at least in places to the open air above the roof, there were wood rat nests, middens, fecal perches and stains. At all four ends of the two clefts, where the cave arches touched the ground, there were middens of feces and food litter coming down out of the crevices like alluvial cones. These indicated the presence of at least two separate dens in each cave. An adult female (480829-1) was shot in the cleft above the west end of the west cave on 29 August 1948. By climbing up the midden and into this cleft I was able to see four nests in niches or on projections of one or the other face of the cleft. All were close enough together to have been under the control of the same rat. Numerous thick hard black fecal deposits on projections, and the long dark varnishlike stains below, attested to the old age of the den and the fondness of *arizonae* for high vertical walls.

The vegetation of the flat upland and the steep slopes of the gulch was predominately Utah juniper and sagebrush with associated shrubs. Greasewood and rabbitbrush were more abundant on the bottom of the gulch. Cuttings of juniper needles were the most abundant kind of food litter. A few sticks and roots had been carried into the cleft. There was a considerable amount of old nesting material scattered on perches in the crevice and on the midden. This consisted of shredded bark mixed in the proportions of roughly 85 per cent juniper bark to 15 per cent sagebrush bark.

A much smaller den at Artesia, 11 miles west and 11 miles north of Rangely, was notable for its six foot deep accumulation of sticks that had been cemented into a solid mass by fecal and urinary deposits and penetrated by tunnels. A young adult male (480830-10) was trapped at this den on 30 August 1948.

Shelter was provided by a hogback ridge of conglomerate and interbedded sandstone with an east-west strike and dipping south at about a 45 degree angle. Numerous dens were along the ridge in vertical clefts cutting through it and in diagonal crevices between the more resistent projecting strata of hard rocks. The conglomerate was made up of river gravel with stones ½ to 1½ inches in diameter and occasional petrified logs 6 to 12 inches thick. The vegetation in the vicinity of the den consisted of Utah junipers, a few piñons, many sagebrush, *Cercocarpus intricatus*, spiny hop-sage, a few Mormon tea, and scattered tufts of grass.

The diagonal crevice at this den was 3 to 5 inches wide between a conglomerate layer above and a sandstone layer below. A rough massive fecal deposit in the diagonal crevice at some points filled the crevice from wall to wall and extended down into the vertical cleft below that was stuffed with sticks and consolidated by the fecal deposit. The sticks were mostly of sagebrush and *Cercocarpus intricatus* with a few of piñon. There were also a few piñon cones and *Opuntia* spines. Only a little den material lay scattered in the diagonal crevice. Food litter was scarce, mainly juniper cuttings. There was an old defunct nest of juniper and sage bark buried under sticks and feces.

An exceptionally large and old den 4 miles west and 2 miles south of Cahone was of particular interest because it had a midden half filling an ancient Pueblo storage chamber. The main part of the den was under a huge block of sandstone greater than 30 feet long, 20 feet high on the uphill side, and 35 feet high on the downhill side of the block. The Pueblo storage chamber was in a cavelike concavity under the upper west side of the rock. On 2 August 1949 a lactating female (490802-1) was trapped on a midden under the lower side of the block. The habitat of this den, on the north rim of Cahone Canyon is described on page 362.

The Pueblo chamber was a round rock cavity approximately 5 feet high and 6 to 10 feet deep (back end not visible to me). The entrance was 3 feet high and walled in from each side with Pueblo masonry to make a narrow doorway. The chamber had probably been constructed by the Pueblo people for storage of corn. In more recent years wood rats had filled it to a depth of 28 inches with a midden consisting mostly of piñon needles, rat feces, and serviceberry twigs. The top of the midden formed an undulating floor that had been cemented by urine and feces to a hard crust. Since its formation, the front part of the midden had been dug out of the chamber for a distance of 3 feet back into the chamber and to a depth of a foot below the crust. There were no tunnels in the midden, and the excavation had the appearance of being done by some predator or man. Spider webs farther back in the Pueblo chamber and the scarcity of fresh food litter indicated that this part of the den was little used at the time of inspection.

The midden in the chamber extended out the doorway and joined another large midden down the slope in a space under the overhanging west side of the sandstone block. This midden was 7½ feet long, 34 inches wide and roughly a foot deep. It had the same composition as the midden in the Pueblo chamber with the addition of sticks and was entirely loose, without any crust or consolidated fecal deposit. On the lower south side of the slope the block rested on several small boulders between which there were small amounts of midden and a few scattered sticks. The immense volume of food litter (primarily piñon needles and serviceberry twigs and leaves) and rat pellets at this den greatly exceeded the amount of miscellaneous den materials accumulated. The latter consisted of scattered sticks, a single dry joint of hunger cactus, 6 corrugated potsherds, and 3 black-on-white potsherds.

Three days later an adult female *arizonae* (490805-1) was trapped a half mile farther east at a den in horizontal and vertical crevices in the sandstone rim of the canyon. The long horizontal crevice in which the rat was caught varied from 9 to 1 inches in height and contained no den material other than food litter, rat pellets, and a few small stones. This crevice was interconnected through others to a wide low vertical cleft in the top layer of sandstone which contained a pile of sticks nearly two feet high. The lower crevices probably were only accessory spaces used by the rat living under the stick pile 15 feet above. Included with the sticks there were two bones (a calcaneum and a first rib) from a Ute Indian who had been buried many years before in the wide cleft a short distance away. All that I saw remaining at the original burial site were three small bones, a tooth, a scrap of cloth, a blue bead, a few small pieces of a modern pottery bowl, and several pieces of harness leather.

An adult female *N. c. rupicola* (500601-1) with two suckling young occupied a good den with numerous deep narrow inaccessible crevices 21 miles north and 5 miles east of Stoneham. The crevices were in soft, roughly sculptured sandstone of the Ogallala formation forming the rim of the High Plains. The topography and vegetation are described in more detail in the habitat section (page 362). The main crevice was a narrow vertical crack from the top to the bottom of the exposure. Narrow horizontal crevices on each side of the vertical one, and the spaces between small broken blocks at the base of the outcrop, provided additional passages and living space. Not much den material or food litter was visible. There were a few dry weed stalks, twigs, and small stones in crevices and on small exposed ledges. An old nest made of yucca fibers was on a shelf close to the vertical crevice. The two young rats were heard squeaking on a shelf 20 feet east of the main cleft and approximately 12 feet above the mouth of a small cave.

A den with a large store of hackberry leaves and cuttings was in a long narrow diagonal crevice that extended through the length of a large block of sandstone that had fallen from the rim. The crevice was about 20 feet long and open only at the two ends. Some space underneath the block may have been used as part of the same den. The only den materials in the crevice or on the ground at either end were dry weed stalks, a few small sticks and stones, and a piece of bone. The crevice contained two bushels of hackberry cuttings that had been gathered the preceding year, as indicated by the mature size of the leaves and the abundance of small leaf galls. Leaves of the current year on the trees were smaller, still growing, and had not yet developed any galls. A hackberry tree standing two and a half feet from the upper end of the crevice was half dead from pruning of its branches by wood rats and gnawing of its bark by wood rats and porcupines. Although I obtained no wood rat at this den, the only kind of *Neotoma* known to occur in that area is *N. c. rupicola.*

FOOD

The diet of the bushy-tailed wood rat is extremely varied as to kinds of plants eaten. The bulk of the staple food items is not provided by any single or few kinds of plants. The bushy-tailed wood rat is noteworthy rather for its versatility in subsisting on whatever kinds of flowering plants may be easily available. There is, however, a definite preference for the foliage rather than the fruits, flowers, stems, or woody parts of the available plants. There is also a distinct preference for the foliage of shrubs and forbs, rather than that of grasses. The succulent joints of cactus are eaten to a limited extent.

The leaves of shrubs seem to provide the greatest proportion of food. The leaves of forbs are almost as frequently eaten, if not more so. Needles of conifers are important foods, although usually consumed in less amount than leaves of shrubs or forbs. Juniper berries, conifer seeds, mushrooms, and the fruits and seeds of other plants are eaten when in season and may have nutritional importance greatly exceeding their bulk in the diet, but they seem never to equal the amount of leaves eaten.

The common sagebrush, one of the most abundant shrubs west of the Continental Divide from the lowest valleys to nearly 10,000 feet in the mountains, is among the shrubs least desired as food by the bushy-tailed wood rat. Nearly all records of sagebrush in the food litter are based on one or a few floral cuttings. The leaves seem to have been eaten only rarely. This aversion to leaves of sagebrush applies generally to other shrubby and herbaceous species of sage (*Artemisia*), but leaves of at least one herbaceous sage (*Artemisia* cf. *A. ludoviciana*) were a well-liked food of *N. c. rupicola.*

The wide variety of plant species eaten by *Neotoma cinerea* is a natural consequence of its wide distribution, there being one or another subspecies present in Colorado in every life-zone from the Arctic-Alpine above timber-line to the Upper Sonoran in McElmo Canyon. At any one locality, of course, the habitats and choices of food are much more restricted. In general, the rats at any given locality feed mostly on the plants that are most abundant and accessible at that locality. This is largely a matter of uncritical requirements and sheer laziness. But adaptive differences in food preferences may have become established between the subspecies *orolestes* and *arizonae.* The former, which occurs above 7000 feet, seems to prefer plants characteristic of the higher elevations, whereas the latter, which occurs below 7000 feet, seems to prefer plants characteristic of the lower elevations. Some plants which are abundant at lower elevations and occur sporadically at higher elevations, such as *Rhus trilobata, Quercus gambellii, Opuntia,* and *Yucca,* are more preferred by *arizonae* than by *orolestes.*

The food preferences of *N. cinerea* are less specialized than those of *N. albigula* and *N. micropus,* resembling most nearly those of *N. mexicana.* From detailed examinations of food material at 58 dens of bushy-tailed wood rats, it is evident that more than 75 per cent of the species of woody plants or forbs available to the rats were eaten, to at least a slight extent. More extensive studies would undoubtedly increase this percentage, and might finally add all available woody plants and forbs to the list of plants actually eaten. A considerable number of grasses, fungi, and other plants also would be added to the list. But the principal significance of food preferences lies not in the variety but in the quantities of each item eaten, with reference to the season and immediate availability. A quantitative evaluation of the food data shows that although almost any flowering plant may be an acceptable food, only a small proportion of them are preferred foods and provide the bulk of the diet. For *N. c. orolestes* these preferred foods are mainly mesophytic shrubs, aspen, and conifers of the Transition and Canadian life-zones. For *N. c. arizonae* the preferred foods are mainly xerophitic shrubs and conifers of the Upper Sonoran Life-zone.

In the present study the data obtained on food can best be presented separately for each subspecies of the bushy-tailed wood rat, because of differences in the available plants in different parts of the range of the wood rat, and because of the few kinds of plants widely available to all three subspecies.

N. cinerea orolestes

Among the most preferred food plants of *orolestes* are the chokecherry, aspen, rose, Douglas-fir, rabbitbrush, mountain lover, Engelmann spruce, pines, junipers, snowberry, squaw currant, and goldenrod. Aspen leaves were usually eaten in considerable quantities, sometimes including the petioles, but the petioles often are left on the twigs. Much bark was frequently eaten off aspen twigs. Bark was gnawed from twigs of squaw currant, and in one instance from those of skunkbush. At one den containing more than a gallon of Douglas-fir cuttings there were among the cuttings 66 bare twigs from which almost all the bark had been eaten.

The following plants seem to be but little used as food by *N. c. orolestes*, even when easily accessible close to a den: *Quercus gambellii, Chrysopsis, Rubus strigosus, Rhus trilobata,* and *Holodiscus dumosus.*

The choice of food eaten by a wood rat depends upon numerous variable factors, of which some of the more important are locality, season, availability of plants, physiological condition of the rat, and individual whim. In order that as many as possible of these factors may be considered in the interpretation of the food data, information concerning food is presented in the following paragraphs for each of 42 dens examined, arranged under the appropriate locality, date, and field number. Names of plants found as food litter are preceded by symbols indicating relative abundance in the litter as follows: ++ nearly all, + large amount, * moderate or unspecified amount, - small amount, -- very little. Names of plants growing within 100 feet of the den but not used as food are listed following the semicolon and without symbols.

Gold King Mine, 9500 Feet

4 July 1949.—490704-1. * *Symphoricarpos utahensis,* * *Rubus strigosus,* * *Picea engelmanni,* * *Populus tremuloides,* - *Smilacina stellata; Picea pungens, Ribes montigenum, Rubus parviflorus, Sambucus pubens, Geranium richardsonii.* The only blue spruce within 100 feet of the den was a three foot sapling with upper branches severely pruned. *Abies lasiocarpa, Pseudotsuga taxifolia,* and *Alnus tenuifolia* grew at distances greater than 100 feet from the den and were not represented in the food litter.

5 July 1949.—490705-1. + *Abies lasiocarpa,* + *Pachystima myrsinites,* * *Psuedotsuga taxifolia,* * *Picea engelmanni,* * *Populus tremuloides,* * *Picea pungens,* * *Symphoricarpos utahensis,* -- *Sambucus pubens; Alnus tenuifolia, Rubus strigosus, R. parviflorus, Ribes montigenum, Geranium richardsonii.* The only blue spruce within 100 feet of this den was the same pruned sapling recorded near the preceding den. Cuttings of alpine fir, Engelmann spruce, and Douglas-fir must have been cut from trees more than 100 feet from the den. Most of the cuttings of alpine fir and Douglas-fir had their needles uneaten, but most of the needles had been eaten off the Engelmann spruce twigs.

490705-2. * *Pachystima myrsinites,* * *Populus tremuloides,* -Graminae, -- *Picea pungens; Salix* sp., *Symphoricarpos utahensis, Ribes montigenum, Rubus strigosus, Sambucus pubens, Lonicera involucrata, Fragaria, Smilacina stellata.* A solitary willow not far from the den had been pruned. *Pachystima* could not be found growing closer than 120 feet from the den.

490705-3. + *Pachystima myrsinites,* + *Populus tremuloides,* * *Picea engelmanni,* * *Abies lasiocarpa; Picea pungens, Symphoricarpos utahensis, Ribes* *montigenum, Sambucus pubens, Rubus parviflorus, R. strigosus, Geranium richardsonii.* The twigs of mountain lover must have come from plants more than 120 feet from the den. Approximately a pint of Engelmann spruce cuttings had been carried from a distance greater than 100 feet from the den.

Six and One-half Miles Southwest of Silverton, 10,100 Feet

19 July 1949.—491719-9. * *Ribes,* * *Populus tremuloides,* * *Anemone globosa,* * *Sedum integrifolium,* * *Gentiana* cf. *G. parryi,* * *Epilobium angustifolia,* - *Picea engelmanni,* - *Lonicera involucrata,* - *Potentilla,* -- *Symphoricarpos utahensis,* -- *Smilacina stellata,* -- *Valeriana edulis,* -- *Salix; Acer glabrum, Rosa nutkana.* Three kinds of gooseberry (*Ribes inerme, Ribes montigenum* and *Ribes* sp.) were growing in front of the den. All three kinds had been considerably pruned and were probably eaten, but the *Ribes* twigs found with the food litter were not identifiable as to species. Three kinds of willow (*Salix bebbiana, S. brachycarpa,* and *S. pseudomonticola padophylla*) grew within 100 feet of the den. A dense clump of *S. bebbiana* grew immediately in front of the ledge sheltering the den. The only remains of willow in the food litter was a single twig unidentifiable as to species.

Three Miles North of Almont, 8300 Feet

17 July 1948.—480717-1. * *Populus tremuloides,* * *Rosa* cf. *R. nutkana,* * *Ribes cereum,* * *Pinus ponderosa; Artemisia tridentata, Amelanchier alnifolia, Juniperus communis, Solidago missouriensis.* A squaw currant bush directly before the den had been considerably pruned. Serviceberry bushes downslope from the den had been pruned. Bundles of ponderosa pine needles in the food litter had some needles partly eaten.

480717-2. * *Eriogenum cernuum,* * *Picea pungens,* * *Pinus ponderosa; Populus tremuloides, Juniperus scopulorum, Artemisia tridentata, Ribes cereum, Rosa* cf. *R. nutkana, Symphoricarpos tetonensis.* Cones from the ponderosa pine came from at least 150 feet away. No blue spruce, from which the spruce cones in the midden could have come, was seen near the den. *Rosa, Ribes,* and *Symphoricarpos* bushes were pruned, but no cuttings of these were in the food litter.

480717-5. * *Juniperus scopulorum,* * *Ribes cereum,* * *Berberis repens,* - *Artemisia frigida,* - *Chrysothamnus greenei greenei, Picea pungens, Populus tremuloides, Artemisia tridentata.*

20 July 1948.—480720-1. * *Ribes cereum,* * *Rhus trilobata,* * *Artemisia frigida,* * *Berberis repens; Populus tremuloides, Artemisia tridentata, Symphoricarpos tetonensis.* There were sticks of skunkbush with the bark gnawed off.

480720-3. * *Ribes cereum,* * *Rhus trilobata,* * *Chrysothamnus greenei greenei; Populus tremuloides, Artemisia tridentata.*

480720-5. + *Rosa nutkana?,* * *Ribes cereum,* * *Chrysothamnus greenei,* * *C. parryi,* * *Prunus virginiana,* * *Astragalus tenellus,* * *Juniperus scopulorum,* - *Populus tremuloides,* - *Delphinium* sp., - *Chenopodium* sp., -- *Cirsium* sp., -- *Aster,* -- *Solidago,* -- *Artemisia frigida; Rhus trilobata, Artemisia tridentata, Artemisia* (herbaceous sp.), *Berberis repens, Elymus.* Rose leaves were abundant on the midden. Bark of *Ribes* twigs was eaten.

480720-6. * *Prunus virginiana,* * *Elymus* sp., - *Ribes cereum,* - *Chrysothamnus,* - *Astragalus tenellus,* -- *Artemisia tridentata; Populus tremuloides.* Chokecherry and squaw currant bushes had been pruned.

One Mile Southwest of Almont, 8000 Feet

22 July 1949.—490722-1. + *Prunus virginiana,* * *Rosa woodsii,* * *Cornus stolonifera,* * *Artemisia tridentata,* - *Ribes cereum,* - *Amelanchier alnifolia,* - *Juniperus scopulorum,* - *Elymus* sp., -- *Symphoricarpos; Rhus trilobata, Artemisia frigida, Chrysothamnus greenei?, Urtica.* Food litter from sagebrush consisted entirely of flower cuttings. A large clump of chokecherry near the den was heavily pruned. Some serviceberry and dogwood branches also were pruned.

Three Miles East of Gunnison, 7900 Feet

24 July 1949. — 490724-1. + *Juniperus scopulorum,* * *Chrysothamnus greenei?,* * *Chenopodium,* * *Artemisia tridentata,* * *Chrysopsis villosa,* - *Yucca angustissima,* - *Opuntia polyacantha,* -- *Eurotia lanata,* -- *Amelanchier* or *Cercocarpus* (indistinguishable twigs), -- *Polygonum; Artemisia* (herbaceous sp.). It is noteworthy that the food litter was mostly juniper cuttings, although the nearest juniper was 150 feet away. Other food items were of less desired species more characteristic of the low zonal situation, which is marginal for this subspecies.

Six Miles West and Three Miles South of Gunnison, 7600 Feet

24 July 1949.—490724-3. - *Juniperus scopulorum,* - *Artemisia tridentata,* -- *Solidago sparsiflora; Rhus trilobata, Ribes cereum, Artemisia frigida, Opuntia polyacantha, Chenopodium* sp. Some stalks of goldenrod had been snipped from the base of a clump growing close to the den.

490724-6. * *Juniperus scopulorum,* * *Artemisia tridentata,* * *Ribes cereum; Purshia tridentata, Yucca angustissima, Opuntia polyacantha, Artemisia* (2 herbaceous spp.), *Solidago sparsiflora, Chenopodium, Chrysopsis villosa.* Remains of sagebrush in the food litter were entirely flower cuttings. Juniper, squaw currant, and goldenrod had been pruned in the close vicinity of the den.

26 July 1949.—490726-2. + *Juniperus scopulorum,* * *Artemisia tridentata,* * *A. frigida?,* * *Solidago sparsiflora; Rhus trilobata, Ribes cereum, Opuntia polyacantha, Chenopodium* sp., *Chrysopsis villosa.*

Thirty Miles West and Two Miles North of Saguache, 9800 Feet

31 July 1948.—480731-1. - *Ribes cereum,* - *Pseudotsuga taxifolia,* - *Pinus aristata; Artemisia frigida.* A Douglas-fir cutting had some needles eaten off. Cones of Douglas-fir and bristlecone pine probably provided seeds for the wood rat but these may have been eaten by chickarees or some other rodent.

480731-4. * *Populus tremuloides,* * *Holodiscus dumosus,* - Graminae, -- Agaricaceae, -- *Artemisia frigida; Pseudotsuga taxifolia, Picea pungens, Ribes cereum, Rosa* sp. There was a flower cutting of mountain sage.

Twenty One and One-half Miles West and Four and One-half Miles North of Saguache, 9300 Feet

28 July 1949.—490728-5. + *Rosa nutkana,* + *Ribes cereum,* * *Pseudotsuga taxifolia,* - *Pinus ponderosa,* - *Picea pungens,* - *Populus tremuloides,* -- *Hymenoxys richardsonii; Rubus strigosus, Chrysothamnus greenei?, Ribes inerme, Artemisia fridiga?, Potentilla fruticosa, Geranium.* Cuttings of *Ribes inerme* were seen at a nearby den.

Twenty Miles West and Three Miles North of Saguache, 9000 Feet

1 August 1948.—480801-1. * *Ribes cereum,* * *Rhus trilobata,* * *Yucca glauca,* * *Artemisia dracunculus glauca,* - *Potentilla,* - *Pinus aristata,* -- *Pseudotsuga taxifolia,* -- *Senecio; Pinus ponderosa, Lepidium alyssoides.* Leaf blades of soapweed were cut into pieces, fruit capsules gnawed, and many of the seeds eaten.

Three Miles South and Six and One-half Miles East of Crested Butte, 9200 Feet

9 August 1948.—480809-1. + *Pseudotsuga taxifolia,* + *Symphoricarpos,* * *Agropyron* cf. *A. trachycaulum,* * *Rosa,* * *Chenopodium* sp., * *Holodiscus dumosus; Picea pungens.* Scattered among masses of needle cuttings were 66 twigs of Douglas-fir 1 to 5½ inches long with nearly all bark gnawed off.

10 August 1948.—480810-1. + Graminae, * *Populus tremuloides,* -- *Pseudotsuga taxifolia; Ribes cereum, Symphoricarpos* sp., *Amelanchier pumila, Artemisia tridentata.* There were aspen leaves and twigs with bark gnawed off.

480810-2. + *Prunus virginiana,* + *Symphoricarpos* sp., + *Scrophularia lanceolata,* * *Acer glabrum,* * *Smilacina stellata,* * *Rosa* sp., - *Chenopodium* sp., - *Artemisia tridentata,* - *Ribes* sp., - *Aster glaucodes?,* -- *Aster rubrotinctus,* -- *Geranium* sp.; *Holodiscus dumosus, Amelanchier pumila.* Most of the food litter consisted of leaf cuttings of chokecherry from a dense screen of bushes in front of the den. These bushes and the few of *Holodiscus* among them were heavily pruned, but *Holodiscus* was not present in the food litter.

Two Miles South and Nine Miles East of Crested Butte, 9500 Feet

20 August 1948.—480820-1. * *Ribes cereum,* * *Rosa,* sp., * *Symphoricarpos* sp., * *Chenopodium rubrum,* - *Holodiscus dumosus,* - *Lathyrus* sp.; *Pseudotsuga taxifolia, Acer glabrum, Berberis repens.* Creambush had been pruned.

23 August 1948.—480823-1. + *Pseudotsuga taxifolia,* * *Symphoricarpos* sp., * *Rosa* sp., * *Pachystima myrsinites,* * *Ribes cereum; Populus tremuloides, Holodiscus dumosus, Rubus strigosus.* Mountain lover growing 50 feet from the den was considerably pruned. Rose, squaw currant, and snowberry were also pruned.

480823-2. * *Pseudotsuga taxifolia,* * *Lathyrus* sp., *Graminae; *Populus tremuloides, Ribes cereum, Holodiscus dumosus, Artemisia tridentata, Symphoricarpos,* sp., *Artemisia* (2 herbaceous spp.).

480810-7. * *Pseudotsuga taxifolia,* * *Populus tremuloides,* * *Symphoricarpos* sp., * *Amelanchier pumila,* - *Berberis repens,* - *Rosa* sp., - *Pachystima myrsinites,* - *Ribes cereum,* -- *Solidago* sp.; *Holodiscus dumosus, Artemisia tridentata.* Serviceberry and creambush were pruned.

11 August 1948.—480811-1. + Graminae, * *Populus tremuloides,* - *Symphoricarpos; Pseudotsuga taxifolia, Rosa* sp., *Ribes cereum, Amelanchier pumila, Artemisia tridentata.* Nearly all the bark had been eaten off some aspen sticks. Rose and snowberry bushes had been pruned.

480810-4. + *Symphoricarpos* sp., * *Rosa* sp., * *Solidago* sp., - *Berberis repens,* - *Ribes cereum,* - *Populus tremuloides,* - *Artemisia tridentata; Holodiscus dumosus, Arctostaphylos uva-ursi.* A thicket of creambush had been slightly pruned, but no debris of this plant was found at the den.

480810-5. + *Symphoricarpos* sp., * *Ribes cereum,* * *Aster glaucodes,* * *Holodiscus dumosus,* - *Rosa* sp., - *Acer glabrum,* -- *Pseudotsuga taxifolia; Artemisia frigida.* Squaw currant had been severely pruned and the bark eaten off the branches. Creambush had been considerably pruned. Aspens grew approximately 100 feet downslope from the den.

One Mile East and Seven Miles North of Hermosa, 8100 Feet

12 Sept. 1949.—490912-1. * *Juniperus scopulorum,* * *Smilacina stellata,* * *Prunus virginiana,* * *Quercus gambellii,* * *Pinus ponderosa,* * *Pseudotsuga taxifolia,* - *Pinus flexilis,* -- *Ceanothus fendleri,* -- *Rosa nutkana,* -- *Amelanchier alnifolia,* -- *Geranium fremontii cowenii,* -- *Acer glabrum; Artemisia frigida, Brickellia californica, Rhus radicans, Aquilegia caerulea, Berberis repens.* On a ledge just under the roof of the cave in which this den was situated there were 88 dry mushrooms and some leaf cuttings, mostly *Smilacina.* The other food items listed were found at the den on the floor of the cave, 125 feet back from the mouth of the cave. Plants recorded as available to this rat were growing within approximately 100 feet of the mouth of the cave.

Ten Miles East and 15 Miles North of Dolores, 8250 Feet

18 October 1949.—491018-1. + *Prunus virginianus,* + *Rosa sp.,* + *Crataegus,* + *Cirsium,* * *Rhus radicans,* * *Solidago* sp., * *Brickellia* sp., * *Humulus americanus,* - *Smilacina* sp., - *Potentilla hippiana,* - *Galium,* -- *Potentilla gracilis,* -- *Senecio spartioides,* -- *Symphoricarpos; Populus tremuloides, Pinus ponderosa, Quercus gambellii, Amelanchier, Lathyrus* sp., *Berberis repens, Berberis fendleri.* There was not much litter from food already consumed; most of the material consisted of freshly dried cuttings with the leaves uneaten, amounting to more than three gallons.

Two Miles North of Ridgway, 7200 Feet

1 November 1949.—491101-1. + *Opuntia polyacantha,* * *Juniperus utahensis,* * *Cercocarpus montanus,* - *Pinus edulis,* - *Atriplex canescens,* -- *Chrysothamnus nauseosus; Amelanchier, Quercus gambellii, Ephedra viridis, Artemisia tridentata, Gutierrezia, Prunus virginiana, Rhus trilobata, Yucca* sp., *Artemisia frigida, A. ludoviciana, Chrysopsis* sp. Cactus spines were abundant but did not compare with the quantities usually found at dens of the white-throated wood rat.

Two Miles West and One Mile South of Chromo, 7200 Feet

16 November 1949.—491116-2. * *Populus angustifolia,* * *Salix,* * *Melilotus,* - *Rosa* sp., - *Arctium minus,* -- *Prunus virginiana,* -- *Geranium; Juniperus scopulorum, Quercus gambellii, Alnus tenuifolia, Rhus trilobata, Ribes* sp., *Clematis occidentalis, Artemisia frigida, Marrubium vulgare, Achillea lanulosa, Aster glaucodes?, Salsola kali, Chrysopsis.* There were several seed heads of burdock in the food litter, but no leaves.

Four Miles West and Eight Miles South of Craig, 6400 Feet

2 September 1948.—480902-7. + *Chenopodium,* * *Chrysothamnus nauseosus,* * *C. nauseosus albicaulis,* * *Aster rubrotinctus,* * *Salsola kali,* - *Artemisia tridentata,* - *Bromus,* - *Clematis columbiana,* - *Stanleya* sp., -- *Atriplex canescens canescens; Sisymbrium.*

480902-8. + *Chrysothamnus nauseosus speciosus*, + *C. nauseosus albicaulis*, + *Atriplex canescens canescens*, * *Eurotia lanata*, * *Artemisia tridentata*, * *Stanleya* sp., * *Salsola kali*, * *Heuchera parvifolia*, - *Pachystima myrsinites*, - *Symphoricarpos*, - *Astragalus*, - *Prunus virginiana*, -- *Amelanchier; Artemisia* (herbaceous sp.). Seven of the thirteen kinds of plants recognized in the food litter were not observed within 100 feet of the den. Most of these (*Amelanchier, Prunus, Pachystima,* and *Heuchera*) probably were carried at least 200 feet from the opposite cooler slope of the gulch.

Sixteen Miles North of Craig, 6600 Feet

2 September 1948.—480902-13. + *Purshia tridentata*, * *Artemisia tridentata*, * *Atriplex canescens canescens*, * *Chrysothamnus nauseosus graveolens*, * *Opuntia polyacantha*, - Graminae.

3 September 1948.—480903-1. + *Purshia tridentata*, * *Chrysothamnus* sp. (*greenei* or *viscidiflorus*), - *Artemisia tridentata*, - *Salsola kali*, - *Opuntia polyacantha*, - *Astragalus*, - *Aster rubrotinctus*, - *Barbarea; Cirsium undulatum, Lupinus* sp. Of *Aster*, only flowers were found as food litter.

480903-2. - *Artemisia tridentata*, - *Purshia tridentata; Chrysothamnus nauseosus graveolens, Atriplex canescens canescens.* The principal crevices of this den, probably containing most of the food debris, were inaccessible.

480903-3. - *Artemisia tridentata*, - Graminae; *Chrysothamnus nauseosus graveolens, Cirsium undulatum.* Food litter was very scarce.

480903-4. + *Chrysothamnus nauseosus graveolens*, + *Astragalus* sp., + *Lupinus* sp., * *Orthocarpus* sp., * *Lithospermum*, * *Salsola kali*, - *Artemisia tridentata*, - *Opuntia polyacantha*, - Graminae, -- *Gnaphalium* sp., -- *Iva axillaris; Cirsium undulatum.* Rabbitbrush and Russian thistle had been pruned. The lupine leaves must have come from more than 100 feet from the den.

A summary of food data obtained at all 42 dens of *N. c. orolestes* is presented in Table 6 in order to show the relative preference for each kind of food plant. High relative preference is indicated by high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants to the dens were also considered in arranging the plants roughly in order of decreasing preference.

Two wood rats of this species were obtained in November 1949 one mile northeast of Bowie, where seven dens were briefly examined but not studied in detail. The Utah juniper was the dominant plant at this locality and cuttings from it, together with those of *Marrubium vulgare*, were the most common food item at the seven dens. Cuttings of *Atriplex canescens* and *Rhus trilobata* and joints of *Opuntia fragilis* were less common food remains.

Two adult wood rats were trapped at the same den three miles west of San Acacio on 27 May 1950. Most of the food litter at this den consisted of cuttings of piñon and joints and spines of *Opuntia polyacantha albispina*. There were some cuttings of sagebrush and a few blades of *Yucca glauca*. *Juniperus monosperma* was available on this hillside but not represented in the food litter. The den was not studied in detail.

In the summers of 1948 and 1949, bushy-tailed wood rats were live-trapped

Table 6.—Plants Available and Used as Food at 42 Dens of N. c. orolestes (plants listed roughly in order of relative preference)

Plants	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Prunus virginiana	9	8 (89%)	2
Pseudotsuga taxifolia	14	12 (86%)	2
Rosa	18	14 (78%)	1
Chrysothamnus	18	14 (78%)	1
Pinus	11	9 (82%)	
Juniperus	11	9 (82%)	
Symphoricarpos	20	14 (70%)	
Ribes cereum	23	16 (70%)	
Populus tremuloides	23	13 (57%)	1
Pachystima myrsinites	3	6 (200%)	1
Solidago	8	6 (75%)	2
Picea engelmanni	1	4 (400%)	1
Astragalus	5	5 (100%)	1
Smilacina	6	5 (83%)	1
Aster	7	6 (86%)	
Abies lasiocarpus	1	2 (200%)	1
Potentilla	5	4 (80%)	
Atriplex canescens	5	4 (80%)	
Salsola kali	5	4 (80%)	
Chenopodium	9	6 (67%)	
Artemisia tridentata	24	15 (62%)	
Opuntia polyacantha	8	5 (62%)	
Berberis	8	4 (50%)	
Picea pungens	8	4 (50%)	
Purshia tridentata	4	3 (75%)	
Acer glabrum	5	3 (60%)	
Cirsium	4	2 (50%)	1
Amelanchier	10	4 (40%)	1
Stanleya	2	2 (100%)	
Eurotia lanata	2	2 (100%)	
Senecio	2	2 (100%)	
Holodiscus dumosus	9	4 (44%)	
Geranium	7	3 (43%)	
Yucca	4	2 (50%)	
Artemisia frigida	13	5 (38%)	
Rhus trilobata	9	3 (33%)	
Ribes (Grossularia)	9	3 (33%)	
Artemisia (herbaceous spp.)	7	2 (29%)	
Lathyrus	3	2 (67%)	
Salix	3	2 (67%)	
Elymus	3	2 (67%)	
Lonicera involucrata	2	1 (50%)	
Rhus radicans	2	1 (50%)	1
Brickellia	2	1 (50%)	1
Clematis	2	1 (50%)	
Sambucus pubens	4	1 (25%)	
Quercus gambellii	4	1 (25%)	
Chrysopsis	5	1 (20%)	
Rubus strigosus	6	1 (17%)	
Rubus parviflorus	3		

TABLE 6—*Concluded*

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
(single occurrences are listed below and are grouped irrespective of preference)			
Crataegus	1	1	1
Lupinus	1	1	1
Humulus americanus	1	1	1
Orthocarpus	1	1	1
Lithospermum	1	1	1
Heuchera parvifolia	1	1	
Polygonum	1	1	
Melilotus	1	1	
Scrophularia lanceolata	1	1	
Epilobium angustifolium	1	1	
Populus angustifolia	1	1	
Gentiana cf. *G. parryi*	1	1	
Cornus stolonifera	1	1	
Cercocarpus montanus	1	1	
Arctium minus	1	1	
Anemone globosa	1	1	
Gnaphalium	1	1	
Galium	1	1	
Eriogonum cernuum	1	1	
Ceanothus fendleri	1	1	
Sedum integrifolium	1	1	
Delphinium	1	1	
Iva axillaris	1	1	
Valeriana edulis	1	1	
Barbarea	1	1	
Hymenoxys richardsonii	1	1	
Agropyron cf. *A. trachycaulum*	1	1	
Bromus	1	1	
Alnus tenuifolia	1		
Marrubium vulgare	1		
Lepidium alyssoides	1		
Fragaria	1		
Aquilegia caerulea	1		
Urtica	1		
Sisymbrium	1		
Arctostaphylos uva-ursi	1		
Achillea lanulosa	1		
Gutierrezia	1		
Ephedra viridis	1		

at dens three miles north of Almont, 8300 feet elevation, and released at the same place. Repeated observations of these dens were made, at which times the following 27 kinds of plants were recorded as food litter: *Populus tremuloides, Pinus ponderosa, Picea pungens, Juniperus scopulorum, J. communis, Alnus tenuifolia, Prunus virginiana, Rosa nutkana, Ribes cereum, Lonicera involucrata, Chrysothamnus greenei greenei, C. parryi, Artemisia frigida, A. pacifica, Mammillaria vivipara, Heracleum lanatum, Chenopodium, Smilacina stellata, Solidago missouriensis?, Astragalus tenellus, Astragalus* sp., *Aster* sp., *Chrysopsis villosa, Delphinium, Lepidium,* and *Elymus.* In addition to the foregoing kinds of plants, the following nine kinds were available, growing within a short distance of one or more dens, but none of these nine kinds was found as food debris: *Artemisia tridentata, Symphoricarpos tetonensis, Purshia tridentata, Rhus trilobata, Berberis repens, Oenothera coronopifolia, Eriogonum cernuum, Cryptantha fendleri,* and *Bouteloua gracilis.* High significance may be attributed to the absence of sagebrush from the known items, because sagebrush was one of the most abundant shrubs available and was utilized for den and nest material. Most of the other species available were recorded as food at least once from other observations in that area.

Night observations of a young wood rat (Live No. 17) while it was foraging were made on 21 July 1949 three miles north of Almont. The rat was trapped the previous night and kept during the day at camp, where it was weighed (127 grams) and marked. It was a young subadult female, calm and docile, showing little fear of man. No food or water was offered in captivity. After nightfall Mr. Ronald Nabb and I released the rat at the place of capture and watched her activities with the aid of red lanterns. We followed her for 32 minutes and plucked samples of each kind of plant eaten. Comparison of the plucked samples with growing plants was made the following day, and pressed specimens were prepared. The rat ate leaves and tender stems of at least ten kinds of plants, of which the following nine were identified: *Populus tremuloides, Artemisia frigida, A. pacifica, Chrysothamnus parryi, Chenopodium, Oenothera coronopifolia, Eriogonum cernuum, Chrysopsis villosa,* and *Cryptantha fendleri.* This is the only food record that I obtained of *Oenothera coronopifolia* and *Cryptantha fendleri.* In addition to the above plant foods, the rat picked up, nibbled, and discarded the dry remains of a large beetle.

Wood rats trapped alive in July and August, three miles north of Almont, were offered a variety of foods. They eagerly ate quantities of aspen leaves, willow leaves, rose leaves, snowberry leaves, squaw currant leaves and fruit, gooseberry leaves and green fruit, sunflower seeds, and rolled barley. Fruits and leaves of *smilacina stellata* were also eaten, the fruits being preferred over the leaves. The rats ate some leaves of *Lonicera involucrata* but less readily than the above items. Two rats ate a few needles of blue spruce. One rat sniffed the pungent leaves of *Sambucus pubens,* and ate part of a leaf but refused to eat more.

Several bushy-tailed wood rats were watched on 15 and 16 August 1949 inside an abandoned building below the mill of the Gold King Mine. Three of the rats were seen to eat leaves and cuttings of several kinds of plants. Green or freshly dried cuttings of the following plants were lying on shelves and beams inside the building: *Populus tremuloides, Picea engelmanni* (bare twigs), *Abies lasiocarpa, Alnus tenuifolia, Pachystima myrsinites, Symphori-*

carpos utahensis, Sambucus pubens, Smilacina racemosa, Geranium richardsonii (stems with seed spears untouched but leaves eaten), and Agaricaceae (a wet mass of mushrooms and one dry one).

In a smaller building next to the one mentioned above, there was an old assay furnace in which a subadult wood rat lived. The rat was repeatedly observed in its nest in the furnace. Twice on 8 July 1949 (at 11:40 and 17:06) I saw the rat eat leaves and petioles of *Alnus tenuifolia* and leaflets of *Pachystima myrsinites* from fresh cuttings lying about the nest on the furnace grate. On 16 August 1949 recently gathered food cuttings of the following species were recognized on the furnace grate: *Abies lasiocarpa, Picea engelmanni* (twigs), *Berberis repens, Sambucus pubens, Lonicera involucrata,* and *Smilacina racemosa.*

Bushy-tailed wood rats frequently enter camps and buildings and carry off food supplies that are not secured in tight containers. When the mess hall of a boy's camp at the Gold King Mine was re-opened in June 1949 it was discovered that the rats had raided the food storage lockers in the basement and carried off quantities of dried apples and prunes. Poisoned peanut butter was placed in the attic to kill the rats. When I visited the camp in July I entered the attic and found a dead *N. c. orolestes* and several nests with scattered food litter and debris. The native food plants were aspen, one Engelmann spruce twig, mountain lover, and two dry mushrooms. Food debris from the mess hall consisted of dry orange and lemon rinds, dry prunes and pits, a gnawed piece of Cashmere Bouquet soap, and a gnawed turkey bone. No dried apples were found, perhaps all having been eaten during the previous winter.

N. cinerea arizonae

Among the most preferred food plants of *arizonae* are juniper, mountain-mahogany, saltbush, piñon, rabbitbrush, prickly pear, skunkbush, and Russian thistle. The succulent flesh of the prickly pear is eaten, the spine-areoles being left as litter. The foliage of the other plants is eaten.

Information concerning food is presented in the following paragraphs for each of 11 dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Ten Miles West and Five Miles North of Rangely, 5800 Feet

29 August 1948.—480829-1. + *Juniperus utahensis,* * *Sarcobatus vermiculatus,* * *Artemisia tridentata,* * *Atriplex canescens,* - *Rhus trilobata,* - *Artemisia frigida,* - *Chrysothamnus viscidiflorus pumilus,* - *Chrysothamnus nauseosus speciosus,* - *Gutierrezia sarothrae,* - *Opuntia rhodantha?,* - *Echinocereus triglochidiatus; Pinus edulis, Atriplex confertifolia, Amelanchier, Ephedra, Solidago petradoria.* Food remains of sagebrush consisted of flower cuttings. The only bush of *Amelanchier* found near the den was heavily pruned, but no cuttings of this bush were in the food litter.

Eleven Miles West and Eleven Miles North of Rangely, 6000 Feet

30 August 1948.—480830-10. + *Juniperus utahensis,* * *Pinus edulis,* * *Cercocarpus intricatus,* * *Grayia spinosa,* * *Ephedra viridis,* - *Opuntia; Artemisia* *tridentata.* Bushes of *Cercocarpus intricatus, Grayia spinosa,* and *Ephedra viridis* had been pruned.

Two and a Half Miles South of Fruita, 4600 Feet

6 November 1949.—491106-3. * *Eriogonum,* * *Stanleya albescens,* - *Juniperus utahensis,* - *Atriplex confertifolia,* - *Salsola kali,* - *Opuntia rhodantha; Artemisia tridentata, Ephedra viridis, Chrysothamnus greenei, Echinocactus whipplei.*

Four Miles West and Two Miles South of Cahone, 7000 Feet

2 August 1949.—490802-1. + *Pinus edulis,* + *Amelanchier utahensis,* - *Quercus gambellii,* -- *Penstemon bridgesii,* -- *Opuntia polyacantha; Juniperus utahensis, Purshia tridentata, Rhus trilobata, Gutierrezia.*

3 August 1949.—490803-1. + *Pinus edulis,* + *Juniperus utahensis,* + *Amelanchier utahensis,* * *Purshia tridentata,* - *Penstemon bridgesii,* - *Opuntia polyacantha; Rhus trilobata, Quercus gambellii, Yucca baccata, Ephedra viridis, Gutierrezia.*

Three Miles West and Two Miles South of Cahone, 7000 Feet

5 August 1949.—490805-1. * *Pinus edulis,* * *Juniperus utahensis,* * *Cercocarpus montanus; Amelanchier utahensis, Purshia tridentata, Echinocereus coccineus, Penstemon bridgesii, Gutierrezia.*

One and One-half Miles West of Dolores, 7000 Feet

9 September 1948.—480909-1. * *Cercocarpus montanus,* * *Ribes inerme?,* * *Pinus edulis,* * *Gutierrezia,* * *Quercus gambellii,* * *Artemisia frigida,* - *Rhus trilobata,* - *Physalis,* - *Juniperus utahensis,* - *Chrysothamnus nauseosus,* - *Yucca baccata,* - *Sporobolus,* - *Mirabilis multiflora,* -- *Opuntia devisii,* -- *Rosa; Amelanchier, Fendlera rupicola, Artemisia tridentata, Opuntia (Platyopuntia), Bouteloua gracilis.* Although serviceberry (with scrub oak) formed a thicket on the canyon side below the den, no pruned branches were found, and there were no leaves or twigs in the food litter. Food remains of *Physalis* consisted of a few fruit husks and foliage cuttings.

One Mile South and Twenty-two Miles West of Cortez, 5000 Feet

12 September 1948.—480912-6. + *Atriplex confertifolia,* * *Chrysothamnus nauseosus graveolens,* * *Juniperus utahensis,* * *Tetradymia spinosa,* * *Atriplex nuttallii?,* * *Amaranthus albus,* - *Salsola kali,* - *Sporobolus aeroides,* -- *Opuntia,* -- *Ephedra viridis,* -- *Yucca angustissima?,* -- *Gutierrezia; Rhus trilobata, Artemisia tridentata, Aristida fendleriana, Hilaria jamesii.* No growing bush of cottonthorn from which food cuttings could have been obtained was found within 100 feet of the den.

Two Miles South and Twenty-four Miles West of Cortez, 4850 and 5000 Feet.

15 October 1949.—491015-3. + *Sarcobatus vermiculatus,* + *Lepidium lasiocarpum,* * *Salsola kali,* * *Atriplex canescens,* * *Atriplex confertifolia,* * *Senecio longilobus; Tamarix gallica, Populus, Salix, Chrysothamnus nauseosus, Artemisia tridentata, Gutierrezia.* The tamarisks, cottonwoods, and willows grew 50 feet away on the flood bottom of McElmo Creek, below the rim of the bank in which the den was situated.

491015-4. + *Atriplex confertifolia,* * *Rhus trilobata,* * *Chrysothamnus nauseosus,* * *Yucca angustissima,* * *Gutierrezia,* * *Opuntia hystricina,* * *Echinocactus whipplei,* - *Lycium pallidum,* - *Juniperus utahensis; Ephedra viridis, Brickellia scabra, Artemisia tridentata, A. frigida, A. ludoviciana.* The nearest juniper grew 50-60 yards away, and the nearest *Lycium* 100 + feet away. *Echinocactus* areoles were numerous in the midden, but none was seen growing near the den.

Eighteen Miles North and One Mile East of Farmington, 6000 Feet, New Mexico

10 August 1949.—490810-2. + *Atriplex canescens,* + *Rhus trilobata,* + *Amelanchier utahensis,* * *Juniperus utahensis,* * *Clematis ligusticifolia,* * *Artemisia ludoviciana,* - *Pinus edulis,* - *Ribes inerme,* - *Cercocarpus montanus,* - *Artemisia tridentata,* - *Chrysothamnus,* - *Opuntia,* - *Atriplex confertifolia,* -- *Chrysopsis; Forestiera neomexicana, Yucca baccata.*

A summary of food data obtained at all 11 dens of *N. c. arizonae* is presented in Table 7 in order to show the relative preference for each kind of plant.

N. cinerea rupicola

Some preferred foods of *rupicola* (from a study of only four dens) are mugwort, hackberry, and chokecherry leaves. Bark as well as leaves of hackberry was eaten.

Information concerning food is presented in the following paragraphs for each of the dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Twenty-one Miles North and Five Miles East of Stoneham, 4700 Feet

1 June 1950.—500601-1. * *Prunus virginiana,* * *Artemisia* cf. *A. ludoviciana,* - *Rhus trilobata,* - *Opuntia polyacantha; Celtis occidentalis, Ribes aureum, Rhus radicans, Chrysothamnus nauseosus, Yucca glauca, Ribes cereum, Cirsium, Salsola kali, Urtica.* The food litter of skunkbush consisted of fresh flower clusters.

2 June 1950.—500602-1. + *Artemisia* cf. *A. ludoviciana,* * *Opuntia polyacantha,* - *Salsola kali,* -*Prunus virginiana,* - *Mentzelia; Celtis occidentalis, Ribes aureum, Rhus trilobata, Rhus radicans, Chrysothamnus nauseosus, Yucca glauca, Ribes cereum, Cirsium, Urtica.*

500602-2. + *Prunus virginiana,* + *Artemisia* cf. *ludoviciana,* * *Chenopodium,* * *Psoralea linearifolia,* * *Sisymbrium,* - *Chrysothamnus nauseosus,* - *Opuntia polyacantha,* - *Salsola kali,* - *Ambrosia,* -- *Celtis occidentalis; Ribes aureum, Ribes cereum, Rhus trilobata, Rhus radicans, Yucca glauca, Cirsium, Urtica.* *Prunus* and *Rhus trilobata* growing close to the den had been considerably pruned, and *Ribes aureum* had been slightly pruned, but no food debris of the latter two species was found at the den.

500602-4. + +*Celtis occidentalis,* - *Artemisia* cf. *A. ludoviciana,* - *Prunus virginiana,* - *Chrysothamnus nauseosus,* -- *Lappula redowskii; Rhus trilobata,*

TABLE 7.—PLANTS AVAILABLE AND USED AS FOOD AT 11 DENS OF N. C. ARIZONAE (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred	
	within 100 feet of den	as food litter
Juniperus utahensis	9	9 (100%)
Cercocarpus	4	4 (100%)
Atriplex	10	9 (90%)
Pinus edulis	7	6 (86%)
Chrysothamnus	8	6 (75%)
Opuntia (*Platyopuntia*)	9	8 (89%)
Salsola kali	3	3 (100%)
Rhus trilobata	7	4 (57%)
Gutierrezia	8	4 (50%)
Sarcobatus vermiculatus	2	2 (100%)
Yucca angustissima	2	2 (100%)
Ribes	2	2 (100%)
Sporobolus	2	2 (100%)
Artemisia frigida	3	2 (67%)
Quercus gambellii	3	2 (67%)
Penstemon bridgesii	3	2 (67%)
Amelanchier	6	3 (50%)
Artemisia ludoviciana	2	1 (50%)
Echinocereus	2	1 (50%)
Ephedra	6	2 (33%)
Purshia tridentata	3	1 (33%)
Yucca baccata	3	1 (33%)
Artemisia tridentata	8	2 (25%)
Lycium pallidum	0	1*
Tetradymia spinosa	0	1
Echinocactus whipplei	1*	1
Amaranthus albus	1	1
Lepidium lasiocarpum	1	1
Mirabilis multiflora	1	1
Stanleya albescens	1	1
Eriogonum	1	1
Senecio longilobus	1	1
Grayia spinosa	1	1
Clematis ligusticifolia	1	1
Physalis	1	1
Rosa	1	1
Chrysopsis	1	1
Opuntia davisii	1	1
Populus	1	....
Salix	1	....
Tamarix gallica	1	....
Fendlera rupicola	1	....
Forestiera neomexicana	1	....
Brickellia scabra	1	....
Solidago	1	....
Bouteloua gracilis	1	....
Hilaria jamesii	1	....
Aristida fendleriana	1	....

* Single occurrences grouped irrespective of preference.

Ribes aureum, Rhus radicans, Parthenocissus, Cirsium, Urtica, Helianthus. A half dead hackberry tree stood two and a half feet from one end of the long diagonal rock crevice that sheltered the wood rat den. The twigs and branches of the tree had been heavily pruned by wood rats and the bark had been gnawed by wood rats and porcupines.

A summary of food data obtained at four dens of *N. c. rupicola* is presented in Table 8 in order to show the relative preference for each kind of plant. The data are unfortunately too few to allow significant comparisons with other subspecies.

TABLE 8.—PLANTS AVAILABLE AND USED AS FOOD AT 4 DENS OF N. C. RUPICOLA (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Artemisia cf. *A. ludoviciana*	4	4	1
Celtis occidentalis	4	3	1
Prunus virginiana	4	3	1
Opuntia polyacantha	3	3	....
Chenopodium	1	1	1
Psoralea linearifolia	1	1	....
Sisymbrium	1	1	....
Mentzelia	1	1	....
Ambrosia	1	1	....
Lappula redowskii	1	1	....
Salsola kali	3	2	....
Chrysothamnus nauseosus	4	2	....
Rhus trilobata	4	1	....
Helianthus	1	....	....
Parthenocissus	1	....	....
Ribes cereum	3	....	....
Yucca glauca	3	....	....
Cirsium	4	....	....
Urtica	4	....	....
Rhus radicans	4	....	....
Ribes aureum	4	....	....

STORAGE

The bushy-tailed wood rat has a strong instinct for collecting and storing. Large amounts of cuttings of foliage are gathered and stored in late summer and in autumn to provide food for winter use. Small to moderate amounts are sometimes stored at other seasons for temporary needs such as diurnal feeding and to avoid foraging sorties in periods of bright moonlight.

Large stores of food usually are piled or stuffed into large crevices or spaces between boulders, sometimes completely filling them.

Smaller supplies are more haphazard in location. They may fill small crevices, form a layer on the midden, or lie in a pile on top of sticks and other den material. Although large accumulations of cuttings of foliage for seasonal use are always completely dry and well preserved, smaller amounts may be fresh or only partly dried. The smaller amounts of incompletely dried cuttings are probably left in more exposed locations until completely dried or "cured" before being stowed away in the main storage crevices. On the night of 15 August 1949 in an abandoned building at the mill of the Gold King Mine, Colorado, I observed a bushy-tailed wood rat by red light as it carried dry cuttings from the places where they were dried to storage places. Large numbers of cuttings had been spread out on a bench, shelves, beams and the floor, and most of them had dried before the night of observation. The rat made repeated trips carrying cuttings crosswise in his mouth from the bench and beams up the walls and into small openings between the boards just under the roof. Intermittently between trips the rat stopped on a beam near his nest, or on one of the drying places, to eat one or a few dried leaves. The eating of the dried leaves was plainly audible, like a loud rustling or crushing of dry leaves in a person's hand. The rat was selective about eating. He pulled, sniffed, and discarded cuttings until he found a leaf he liked. It was hard to believe that a rat could enjoy such dehydrated fodder while there was still plenty of fresh food outdoors. Among foods he ate that I thought I recognized in the dim red illumination were leaves of aspen and mountain lover. For the kinds of plant cuttings found in the room the following morning see page 388.

Quantities of stored food were found at ten dens of *N. cinerea orolestes*, as described in the following paragraphs. The stores at nine of the dens were almost entirely cuttings of foliage, but the store at the tenth den was mainly of dried mushrooms. No appreciable quantities of fruits, nuts, or seeds were found at any den.

Den 490705-1 contained approximately two gallons of cuttings of alpine fir, Douglas-fir, and mountain lover. At den 490705-3 there was a small pile of approximately one pint of cuttings of Engelmann spruce probably temporary storage for diurnal feeding. At den 490722-1 there was a supply of approximately five gallons of dry cuttings of chokecherry leaves between the talus boulders under which the den was situated. Although the buried dry leaves were still green, the leaves on the surface had turned brown, which indicated that the age of the storage pile probably dated back to the preceding autumn.

More than a gallon of foliage cuttings of Douglas-fir was found at den 480809-1 as a three-inch layer on the upper level of the den. Mixed with the uneaten cuttings there were many bare twigs and twigs with partly-eaten needles. At den 480810-2 the floor of the small cave housing the den had a bed 3 to 4 inches deep of mixed, foliage cuttings. Chokecherry leaves were most numerous, with also large quantities of leaves of snowberry and *Scrophularia lanceolata*, and smaller amounts of other plants.

When rat 480810-4 was trapped on 10 August 1948 there was no stored supply of food visible in the den-crevice. But when the den was examined again on 16 September 1948 there was a pile of approximately a gallon of goldenrod cuttings with a few aspen leaves. This supply must have been gathered by a new occupant of the den since the capture of the previous occupant. Likewise, at den 480810-7, approximately 100 yards from den 480810-4, there was no stored food on 10 August 1948. But on 16 September a pile of approximately a quart of fresh serviceberry cuttings was found on the ground under a bush of *Holodiscus dumosus* approximately 12 feet from the base of the den.

Den 490912-1 was situated under fallen rocks on the floor of a limestone cave. On a narrow ledge under the roof of the cave there was a supply of 88 dried mushrooms (unidentified) and some cuttings, mostly *Smilacina stellata*. The mushrooms were damp and in poor condition and the leaves mildewed from water seeping through the roof of the cave.

At den 491018-1 in the crevices of a sandstone outcrop a mass of at least three gallons of dry green cuttings of foliage partly filled some of the crevices. Almost no leaves had been eaten from these cuttings. Fourteen kinds of plants were mixed together including large amounts of *Prunus virginiana, Rosa, Crataegus,* and *Cirsium.*

At den 480903-4 in the south side of an igneous dike, a rear chamber of the sheltering horizontal crevice was filled with nearly a bushel of dry cuttings. There were large quantities of *Astragalus* and *Lupinus* leaves and considerable amounts of *Orthocarpus, Lithospermum,* and *Chrysothamnus nauseosus graveolens. Lupinus* was available only on the north side of the dike more than 100 feet away from the den.

No stored food was found at any den of *N. c. arizonae.*

Stored food was found at two of the four dens of *N. c. rupicola* examined. Approximately two bushels of dry hackberry cuttings were found at den 500602-4 in June, 1950. The stored material partly filled a diagonal crevice through a large sandstone boulder. The large size of the hackberry leaves and the prevalence of leaf galls, in contrast to the small leaves without galls growing on trees at that time, indicated that this storage supply had been gathered the previous autumn. At den 500602-2 there were approximately four quarts of old, brown, mixed cuttings, probably also dating from the previous autumn. The supply contained mostly chokecherry leaves, and secondly mugwort.

REPRODUCTION AND YOUNG

Information on reproduction of *N. c. orolestes* was obtained from 20 females collected by me. Collectors of other specimens examined did not record such information. Of the 20 females collected, seven were in breeding condition as recorded in the table below. These seven females and numerous young specimens of the immature, subadult, and first year adult age classes from many localities and several months of the year show that *orolestes* breeds in the early summer. So far as previously known, the bushy-tailed wood rat was thought to have but one litter per year (Warren, 1926: 99-101; and Dixon, 1919: 62). But each of two females included in Table 9 was both pregnant and lactating. It is probable, because of the shortness of the season at high elevations, that one litter is the normal number, but two litters are sometimes reared, when conditions are favorable.

TABLE 9.—BREEDING CONDITION OF FEMALES OF N. C. OROLESTES

LOCALITY	Date	Age	Weight	Condition
3 mi. W San Acacio, 8050 ft.	27 May	2nd year adult	254 g	3 emb. 20 mm
8 mi. N, 1 mi. W Hesperus, 9500 ft.	5 July	3rd year adult	310 g	lactating, no emb.
8 mi. N, 1 mi. W Hesperus, 9500 ft.	5 July	2nd year adult	282 g	lactating, 1 emb. 12 mm
3 mi. N Almont, 8300 ft.	20 July	3rd year adult	280 g	lactating, no emb.
3 mi. N Almont, 8300 ft.	20 July	3rd year adult	315 g	lactating, no emb.
3 mi. N Almont, 8300 ft.	22 July	4th year senile	216 g	lactating, 4 emb. 8 mm
3 mi. N Almont, 8300 ft,	23 July	2nd year adult	242 g	lactating, no emb.

Data on the breeding conditions of males are incomplete but suggest that the breeding season ends in August and that the young males of the year do not usually reach sexual maturity before their first winter. This suggestion rests on the assumption that the weights and measurements listed in the table below may be interpreted in the same way as weights and measurements reported by Linsdale and Tevis (1951: 345 and 355) for *N. fuscipes luciana.* Such an assumption is not necessarily true, but the difference in size between these two kinds of rats is slight.

Records of *N. c. arizonae* reported by Warren (1926: 100) and indicated in Table 11 by asterisks show earlier breeding dates than those obtained for *orolestes.* Since Warren did not regularly record breeding information on skin labels, it is not possible to determine the proportion of females collected by him that were in breeding condition. I collected 8 adult and subadult females between 31 July and 6 November, of which only 2, listed in Table 11, were in breeding condition. They may have been nursing their second litters.

TABLE 10.—BREEDING CONDITION OF MALES OF N. C. OROLESTES

LOCALITY	Date	Age	Weight	Condition
8 mi. N, 1 mi. W Hesperus, 9500 ft.	4 July	subadult	140 g	testes abdom.
6½ mi. SW Silverton, 10,100 ft.	19 July	2nd year adult	308 g	testes scrotal
6 mi. W, 3 mi. S Gunnison, 7600 ft.	24 July	2nd year adult	231 g	testes scrotal
32 mi. W, 2 mi. N Saguache, 9800 ft.	31 July	subadult	215 g	testes 6 mm
3 mi. S, 6½ mi. E Crested Butte, 9200 ft.	10 Aug.	2nd year adult	410 g	testes 10 mm
2 mi. N Ridgway, 7200 ft.	1 Nov.	1st year adult	206 g	testes abdom., 6 mm
2 mi. W, 1 mi. S Chromo, 7200 ft.	16 Nov.	1st year adult	231 g	testes abdom., 8 mm

TABLE 11.—BREEDING CONDITION OF FEMALES OF N. C. ARIZONAE

LOCALITY	Date	Age	Weight	Condition
* Cortez, 6250 ft.	4 April	....	....	lactating
* Cortez, 6250 ft.	4 April	....	....	6 embryos
* Cortez, 6250 ft.	6 April	....	....	4 embryos
* Coventry	13 April	....	....	4 embryos
* Coventry	19 April	....	....	lactating
4 mi. W, 2 mi. S Cahone, 7000 ft.	2 Aug.	2nd year adult	224 g	lactating
4 mi. W, 2 mi. S Cahone, 7000 ft.	5 Aug.	3rd year adult	156 g	lactating

The low elevations prevailing in the range of *arizonae* favor early breeding and a long reproductive season. Numerous immature and subadult specimens collected between the middle of May and the middle of September represent litters born in April, May, June, July, and perhaps August.

Breeding records of females of *N. c. rupicola*, listed in Table 12, show that litters were born in late spring. One of the two suckling juveniles of the female from near Stoneham weighed 41 grams on 2 June 1950. The pregnant subadult from near Meriden was in an early stage of the second molt and still retained the exoccipital sutures. I do not think she could have been more than five months old; probably she was less. Thus, the breeding season must begin early in the spring or even in late winter. Lactating females indicated by asterisks were reported by Warren (1926: 101). Lactating females indicated by daggers were reported by Cary (1911: 114).

TABLE 12.—BREEDING CONDITION OF FEMALES OF N. C. RUPICOLA

LOCALITY	Date	Age	Weight	Condition
21 mi. N, 5 mi. E Stoneham, 4700 ft.	2 June	2nd year adult	320 g	lactating, 2 suckling juv.
† near Chimney Cliffs.	4-8 June	. . . .	. . . .	lactating
† near Chimney Cliffs.	4-8 June	. . . .	. . . .	lactating
* Pawnee Buttes.	6 June	. . . .	. . . .	lactating
* Pawnee Buttes.	6 June	. . . .	. . . .	lactating
* Pawnee Buttes.	6 June	. . . .	. . . .	lactating
6 mi. W Meriden, 5200 ft., Wyo.	20 July	subadult	174 g	3 emb. 15 mm

A subadult female was taken on 27 June 1931, one mile north of Geary's Reservoir. Two subadult males were taken on 8 July 1947 at Battle Cañon. Two subadult males weighing 144.7 and 162.8 grams were collected on 20 July 1945 at the same locality as the pregnant subadult. These rats must have been born in April or May.

MOLTS

The patterns of molt in *Neotoma cinerea* are better understood than those of any other kind of wood rat because of the relative abundance of specimens of many ages and nearly all seasons of the year. A general description of the typical pattern of each molt is given in the following paragraphs.

The postjuvenal molt is more constant in pattern than any of the later molts but is, nevertheless, subject to considerable variation. It first appears as a longitudinal band on the midabdomen and spreads laterally up each side of the body. At first only a short "stubble" of new hairs can be seen by ruffling the juvenal pelage. The band of short hairs along each lateral line spreads rapidly fore and aft between the forelegs and hind legs. The new pelage spreads less rapidly forward on the breast, and slowly backward to the inguinal region. On the sides the molt spreads posteriorly over the hind legs and hips and at the same time advances slowly up the sides on a broad front. The new hairs on the abdomen reach full length while the molt is just spreading over the thighs under the longer juvenal pelage. The molt lines from opposite sides first meet dorsally on the rump or lower back when the subadult pelage is growing in thickly on the sides and reaching full length (visible at the surface) low on the sides. At the same time, the new fur grows in thickly on the forelegs, and the molt on the underparts moves forward over the breast.

After the junction of the right and left molt lines on the rump, the molt on the sides continues to spread dorsally and the line across the rump advances forward up the back. From the region of the throat and forelegs the molt spreads up the sides of head, neck, and shoulders while the molt is advancing up the back. The advancing molt lines converge on a small area on the crown or nape, where progress frequently slows almost to a halt for an extended period of time. In late stages of the postjuvenal molt the sides, legs, and hips are covered with bright thick subadult pelage while a roughly triangular area between the shoulders and rump is still clothed only in thin, fuzzy, gray juvenal pelage. The size of the triangle is then reduced to a patch on the head and neck. In most kinds of wood rats this patch persists until after the second molt is well under way.

A distinct postjuvenal molt of the tail was not recognized on study skins, but significant changes deserve mention by which the bushy tail of the adult is acquired. When the postjuvenal molt is progressing on the back, the tail begins to grow bushy. Long stiff dark hairs grow out covering the short soft juvenal hairs, beginning at the base and progressing to the tip of the tail. When these hairs attain full length they stand out from the skin laterally and to a lesser extent dorsally but lie nearly flat on the ventral side of the tail. I could find no indication of a complete molt of the short underlying hairs. The tip of the tail does not become bushy until after the postjuvenal molt is completed on the head and neck. A tuft of soft whitish hairs on the tip of the tail may persist even until the second molt is nearly completed. Hence, such a whitish tip of the tail is a good sign distinguishing a first-year adult from a second-year adult bushy-tailed wood rat.

The pattern of the second molt is, in general, similar to that of the postjuvenal molt. There are too few specimens of proper age and season to permit me to follow the course of the molt in detail. It seems to start along the lateral line or on the belly and to spread almost simultaneously over the abdomen, sides, and legs. Molt lines from opposite sides meet first on the rump and advance up the sides and back to the head, as in the subadult molt. Specimens in the third molt are even fewer than those in the second molt. The lines of the third molt are sometimes narrower and less distinct, even fading out completely, but they seem to progress in the same pattern as the second molt. The second and third molts are both more irregular than the postjuvenal molt.

The pattern of the annual molt is notably irregular. A symmetrical molt line is usually not recognizable. The new incoming hairs may appear in separate patches that spread unevenly. The molt usually begins on the belly and spreads rapidly over the sides, hips, and back, often appearing in two or more places, or over a broad area, at once. A large part of the dorsal surfaces may be in molt at the same time, but with asymmetrical variations in length of the new hairs. The neck seems usually to be the last area to finish the annual molt.

Some specimens are described in order of age in the following paragraphs to illustrate different stages of molt, to present evidence of the existence of the third molt, and to show the kinds of individual variation that occur in molt patterns. The seasonal distribution of specimens in molt is shown in Plate 22.

The earliest state of the postjuvenal molt is shown by a subadult female (KU 29206) from 3 miles south and 6½ miles east of Crested Butte, 10 August 1948. Short stiff hairs of the subadult pelage, mostly less than half the length of the soft overlying juvenal pelage, are growing on the lower sides posteriorly as far as the thighs and across the midabdomen over the area of the dermal gland.

KU 20586, immature female, from ½ mile east and 3 miles south of Ward, taken on 3 August, has the postjuvenal molt beginning over extensive areas of the belly, sides, legs, and rump, but everywhere concealed. More advanced stages of molt are shown by two subadults (KU 29213 and 29218) from three miles north of Almont.

CM 20077, subadult female, from Meeker, 22 July, is in late postjuvenal molt with juvenal pelage remaining on the head, neck, and back, and with two isolated centers of molt, one on each side of the rostrum in the area of the vibrissae.

MVZ 86938, first year adult male, from eight miles northeast of Dove Creek, taken on 3 August, has nearly completed the postjuvenal molt. The subadult pelage is full length over most of the body but remains covered with juvenal hairs on the crown and nape. The tail has become somewhat bushy and is fringed with white at the tip. No evidence of the onset of the second molt was found on the belly, sides, or rump.

An abnormal condition of arrested postjuvenal molt is shown by a subadult female (DM 4404) from Four Corners, taken on 25 July. A conspicuous difference in color and texture distinguishes the juvenal pelage on the head, neck and back from the full length subadult pelage on the sides, legs, and rump (see description of this skin on page 262). But there is no line of molt in progress between the two pelages. The molt had come to a stop and all the short new hairs had grown out to full length by the time the rat was killed. Such a condition occurs normally in most rats at certain places, such as where the juvenal pelage of the inguinal region contacts the molt line of the subadult pelage on the hind leg or flank. Where the two pelages look alike, such a local contact may be almost impossible to detect after the new pelage has reached full length. The progress of molt on the venter of DM 4404 was not fully arrested as it was on the back, for a diagonal band of short new hairs extends across the breast. Molt was still progressing forward on the right side but lagged on the left, with the result that the white "stubble" of new hairs fades out posteriorly on the left side. An additional indication of arrested molt is the condition of the tail, which is in the stage of growing bushy, but still with a white tip. Such a tail would normally go with a molt pattern that had already advanced up the back to the neck, with only a patch of juvenal pelage remaining. A comparison of this specimen with a younger subadult male (DM 4406) from the same place, taken on 21 May, shows that the former was noticeably smaller, both in external measurements and in length of skull. The molt on the latter (DM 4406) is entirely hidden and the tail whitish and soft haired. Conditions of tooth wear and cranial sutures likewise indicate that the smaller rat (DM 4404) with the arrested molt was the older of the two.

A late stage of the postjuvenal molt, simultaneously with an early stage of the second molt, is shown by KU 29219, adult male, from three miles north of Almont, 20 July 1948. This rat weighed 260 grams and had a head and body length of 199 mm. Its third upper molars have barely attained the condition of wear characteristic of an adult, but the exoccipital sutures are still visible. The subadult pelage is not yet full grown on the head, neck and back. An area of gray juvenal pelage overlies the new fur on the crown, nape and upper back between the shoulders. A smaller thin patch of juvenal pelage remains on the middle of the back. New stiff black hairs cover the soft wavy hairs on the proximal half of the tail, but the terminal half of the tail is still tufted with long soft whitish hairs. The second molt is in progress on the abdomen, lower sides, flanks and thighs, with the hairs of the first autumn pelage longest on the midline of the abdomen and shortest on the sides, but nowhere yet visible without separating the hairs of the subadult pelage. KU 29216, adult male, from 2 miles south and 9 miles east of Crested Butte, 23 August 1948, shows later stages of both molts.

I have found no specimens in which the postjuvenal molt has been completed (subadult pelage full length) and the second molt not yet begun. If such an interval sometimes occurs between these molts in this species, it must be short.

KU 15729, subadult female, from six miles west of Meriden, Wyoming, taken on 20 July, is in subadult pelage with no remnant of juvenal pelage remaining on the neck. The second molt is under way in a narrow band along the lateral line and the tail is narrowly bushy and white-tipped.

KU 34832, first year adult male, from 1 mile east and 7 miles north of Hermosa, 12 September, is in full second molt with dark buffy gray subadult pelage on the head, shoulders, back and upper sides. The lower sides, forelegs, flanks, and thighs are rich orange buff, in first autumn pelage. KU 34821, first year adult male, from one mile northeast of Bowie, on 5 November was in far advanced second molt on the back, shoulders, and sides of the face.

At first glance AM 27431, first year adult male, from Irwin, 23 October 1905, appears to be in prime subadult or first autumn pelage. Ruffling of the fur reveals, however, that the second molt was in full progress. First autumn pelage was growing in thickly on the back, upper sides, and shoulders. On the crown, nape, and between the shoulders there is only subadult pelage. New first autumn pelage has replaced the subadult pelage over most of the sides, flanks, legs, and under parts. The two pelages are so alike in color that no difference can be detected on the surface. The tail is fully bushy, but the tip is narrower than in old adults and fringed with whitish. The length of head and body was 213 mm.

Several specimens from Grand Junction collected in late September demonstrate the existence of a third molt in the first year. AM 27429, a first year adult female, shows two molts separating three distinct pelages, none of which is the juvenal pelage. An early molt was nearing completion on the upper back and nape. Only a small area on the crown had not yet begun to molt. The old pelage covering these parts is dull buffy brown without the gray fuzzy appearance of juvenal pelage. The sleek appearance of this old pelage, as well as the dark gray bushy tip of the tail and the condition of the skull, clearly indicate that the old pelage is the subadult pelage, which is undergoing the second molt. The succeeding first autumn pelage is long, sleek, and bright buff, heavily overlaid with black. It covers the lower back, rump, legs and sides. Another zone of molt is concealed along the sides of the belly, extending down the outsides of the thighs, and across the venter between the breast and abdomen. Within this area the belly is covered with new full-length hairs. The most recent molt on the belly and thighs must be the third molt of the year. The pelage it ushers in must, then, be the first winter pelage. Several other specimens of about the same age, collected at Grand Junction at the same time of year, show two molts in progress with characteristics similar to those of AM 27429. In each such specimen the juvenal pelage seems to be lacking. The third molt seems to be of normal occurrence in litters born in early summer of the same year. But it seems doubtful that litters born later in the year pass through a third molt the same year.

Evidence of a third molt was also obtained by live-trapping rats three miles north of Almont. On 13 August 1948, a subadult *N. cinerea* (Live No. 8, female) was caught for the first time. She weighed 180 grams and was in buffy gray subadult pelage with a bushy tail still retaining a tuft of soft juvenal hairs at the tip. The second molt was in progress beneath the surface on the flanks and hind legs. When trapped again on 15 September she weighed 222 grams and had lost the soft tuft on the end of her tail. The second molt had progressed up the sides and back to the head. The first autumn pelage was still short on top of the head, longer down the back, and full length on the rump. The third molt had already begun on the sides of the forelegs and hind legs where short new hairs of the first winter pelage lay close to the skin. Another subadult (Live No. 7) was caught on the same nights and showed similar stages of the second and third molts.

KU 34845, first year adult male, from 2 miles south and 24 miles west of Cortez, 15 October 1949, is in long thick pelage with a bushy tail. The third molt was proceeding slowly and irregularly on the sides, rump and lower back. In some places the molt line of short new hairs is thin and faint or has disappeared where the molt has stopped. There are irregular gradations in brightness of hue on the sides and legs where the new, brighter pelage has attained full length beside duller old pelage. The back, from the lumbar region to the head, is in first autumn pelage and has not begun to molt.

KU 34824, second year adult male, from 6 miles west and 3 miles south of Gunnison, 24 July 1949, is in long moderately worn pelage, with annual molt barely beginning only on the venter.

KU 37143, second year adult female, from three miles west of San Acacio, 27 May 1950, is in worn pelage. Short new pelage, less than one fourth the length of the overlying worn pelage, is growing in on the rump. There is a trace of molt beginning also on the left side, but no indication of molt on the rest of the back, the thighs, right side, or under parts. This rat contained three embryos. It is surprising to find a female in active reproductive condition beginning the annual molt so early in the year.

DM 3333, second year adult male, from one mile southwest of Fruita, 22 July 1938, is in heavy and irregular annual molt over the back and sides. The new pelage on the sides is highly irregular in length, some spots having fur of nearly full length, and other spots having only extremely short fur covered by the old pelage.

Some live rats trapped and released three miles north of Almont were dyed with Roux oil shampoo tint to aid in recognition of pelages. Recaptures of dyed wood rats confirmed the belief that adults have only one molt per year, and showed that the hairs of the bushy tail are completely replaced at the annual molt. An old adult female (Live No. 1) was in rough worn pelage when first examined and dyed on 22 July 1948. She had not begun to molt. On 15 September the annual molt was well along toward completion. There was a blackish wash of dyed hairs on the back and sides interspersed with new grayish hairs. On the neck and back of the head the new hairs were only half length. The belly was white with a zig-zag blackish band down each side covering shorter white hairs of the new pelage. The tail was mixed blackish and normal, and the feet were white. I dyed her again before release. When this rat was recaptured on 22 July of the following summer, some dyed fur still remained, mostly on the belly. The tail was gray dorsally with an irregular brownish wash of dye on the underside mixed with white. Much of the irregularity of the dye resulted from the rat having been dyed in the fall before the new pelage was fully grown.

A live adult female (Live No. 5), examined and dyed on 23 July 1948, had begun to molt. New pelage was short on the rump and just coming through the skin on the legs. On 13 August she was still black with dye nearly all over, but had new white hairs sprinkled on the breast, throat, and fore feet. New pelage was beginning to show through the old on the flanks and was long but still covered on all four legs. On 15 September her annual molt was nearly completed. Old dyed pelage was nearly all gone, but for mottled traces on the back, sides, and hind feet. The tail was still nearly all dyed blackish, but the underside of the tail had turned white for about 1½ inches from the base. Only a trace of dye remained on the midbelly, probably on the ends of new hairs that had already sprouted before the rat was dyed. Another adult female (Live No. 4), examined and dyed on 23 July, was in more advanced annual molt. On 13 August her tail was still black, but most of the dyed hair had fallen out of the back and sides. By 15 September only mottled traces of dye remained on the back, probably mostly the dyed tips of new hairs. The tail was gray above, becoming blackish toward the tip, and white below except blackish at the tip. The end of the tail seems to be the last part to finish the annual molt. The two individuals described above indicate that the duration of the annual molt is approximately two months.

KU 29215, second year adult male, from three miles north of Almont, 17 July 1948, seems to have been undergoing two molts. Over the neck and back the new pelage is nearly full length, but still mostly covered by old pelage. On the sides, hips, and rump there seems to be only new pelage. There is a later molt concealed on the breast, lower sides, and hind legs. Most of the belly seems covered by the full length pelage of this more recent molt. The "new" pelage on the shoulders can be traced laterally over the sides to tie in with the "older" pelage on the breast. There is also a concealed molt line across the throat, probably associated with the earlier molt. This rat was probably undergoing two annual molts in quick succession, or possibly an annual molt following an arrested third molt of the previous year.

PARASITES

The kinds of parasites collected from bushy-tailed wood rats in the present study and the field numbers of individual hosts are listed below for each subspecies of wood rat.

Neotoma cinerea orolestes:

Anoplocephalidae

Andrya cf. *A. macrocephala,* 490722-4 (adult tapeworms)

FIG. 1. Low barricade of sticks, bones, and cactus joints gathered by *N. cinerea* (490726-2) 6 miles west and 3 miles south of Gunnison.

FIG. 2. Den of *N. cinerea*, three miles north of Almont, with fecal deposits on projections in vertical cleft.

FIG. 3. Den of *N. cinerea* (Live No. 10) three miles north of Almont. Note cone of sticks at base of crevice.

PLATE 16

FIG. 1. Den of *N. cinerea* (490722-1) under talus blocks one mile southwest of Almont. The cliff exposed to weather has fecal deposits on projecting perches but no dark streaked stains below the perches. The rake handle is 39 inches long.

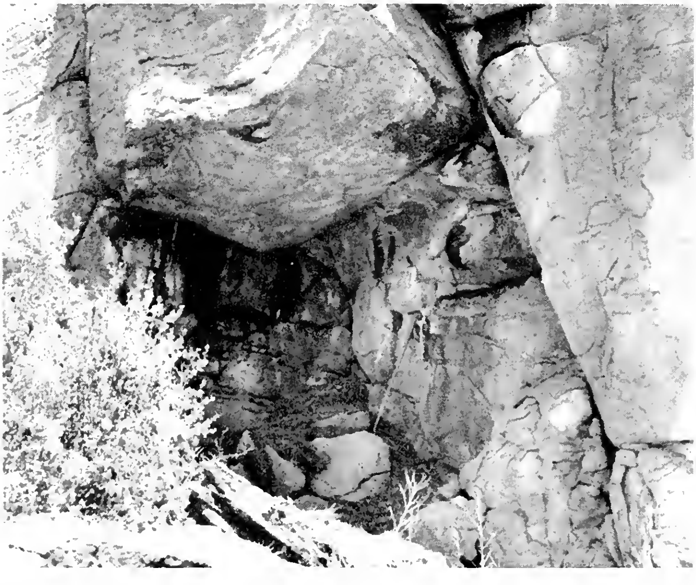


FIG. 2. Den of *N. cinerea* (490728-5) in joints around an overhanging block, 21½ miles west and 4½ miles north of Saguache. Dark stains streak the sheltered walls below crevices and perches.

FIG. 1. Den of N. *cinerea* (490719-9) under limestone outcrop six and a half miles southwest of Silverton. (See Pl. 11, Fig. 1.)

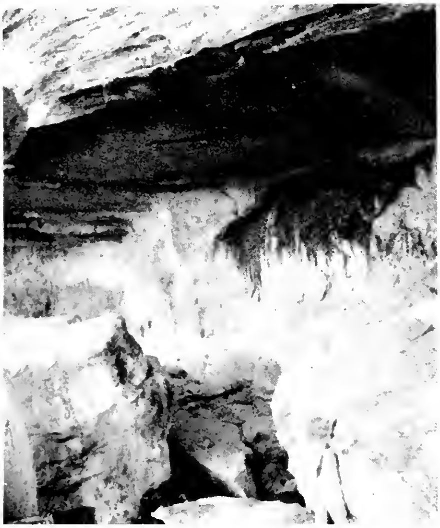


FIG. 2. Fecal deposit of N. *cinerea* on wall under overhanging cliff one and a half miles west of Dolores.

FIG. 3. View into rear end of cave containing stick pile and nests of N. *cinerea* (480720-6). Arrows show locations of nests.

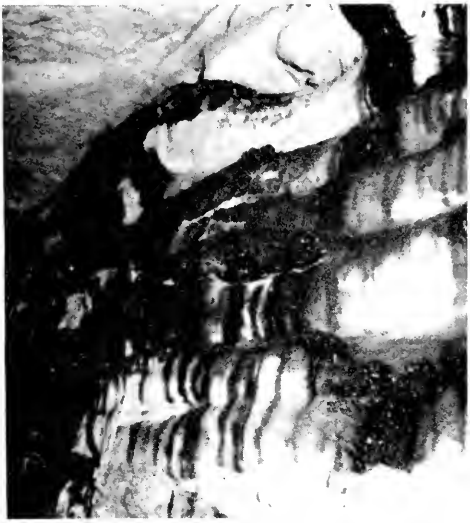


FIG. 4. East wall of same cave as in Fig. 3, showing extensive fecal and urinary deposits below ledges and projections.

PLATE 18

FIG. 1. Den of *N. c. arizonae* (491101-1) beneath overhanging sandstone layer in cliff of interbedded sedimentary rocks two miles north of Ridgway. The dark material on the ledge consisted mostly of small sticks and shredded juniper bark.

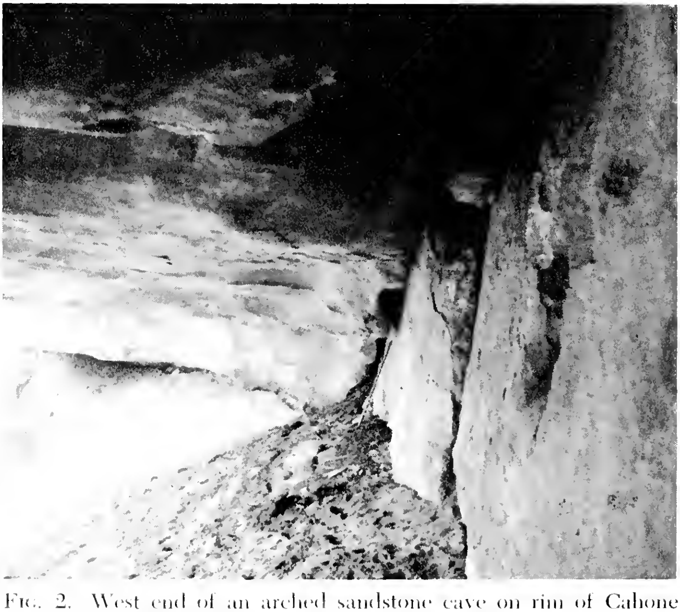


FIG. 2. West end of an arched sandstone cave on rim of Cahone Canyon. Den of *N. cinerea* (490803-1) is in vertical cleft through roof of cave.

PLATE 19

FIG. 1. Den of bushy-tailed wood rat in wall of an ore bin of Gold King Mill (see Pl. 13, Fig. 1). Nests and assorted trash partly filled spaces on beams between the wall boards.

FIG. 2. Den of *N. cinerea* beneath shingle pile and other trash in Gold King Mill. The dark urinary stains on the back wall come from feeding and resting places on a large stringer beneath the floor joists overhead.

PLATE 20

FIG. 1. Domed nest of *N. cinerea* removed from den 490705-3 shown in Plate 9, Fig. 2. The material consisted of cotton wadding and other waste fibers gathered in Gold King Mill.

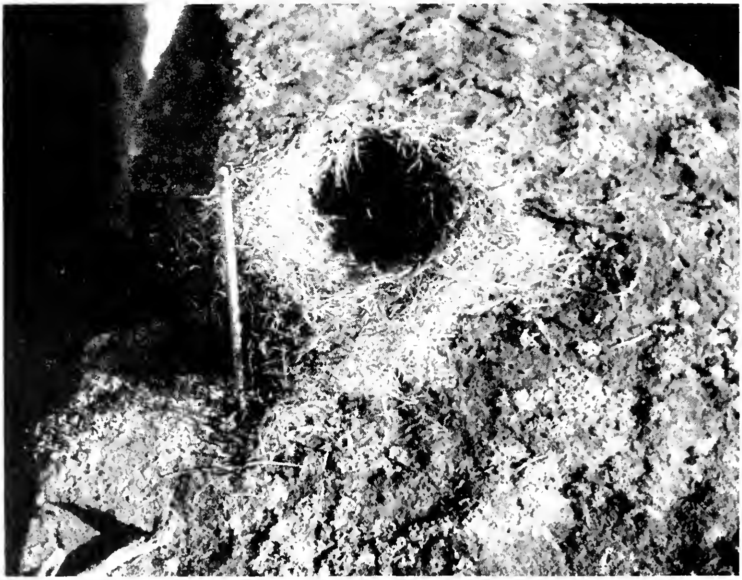
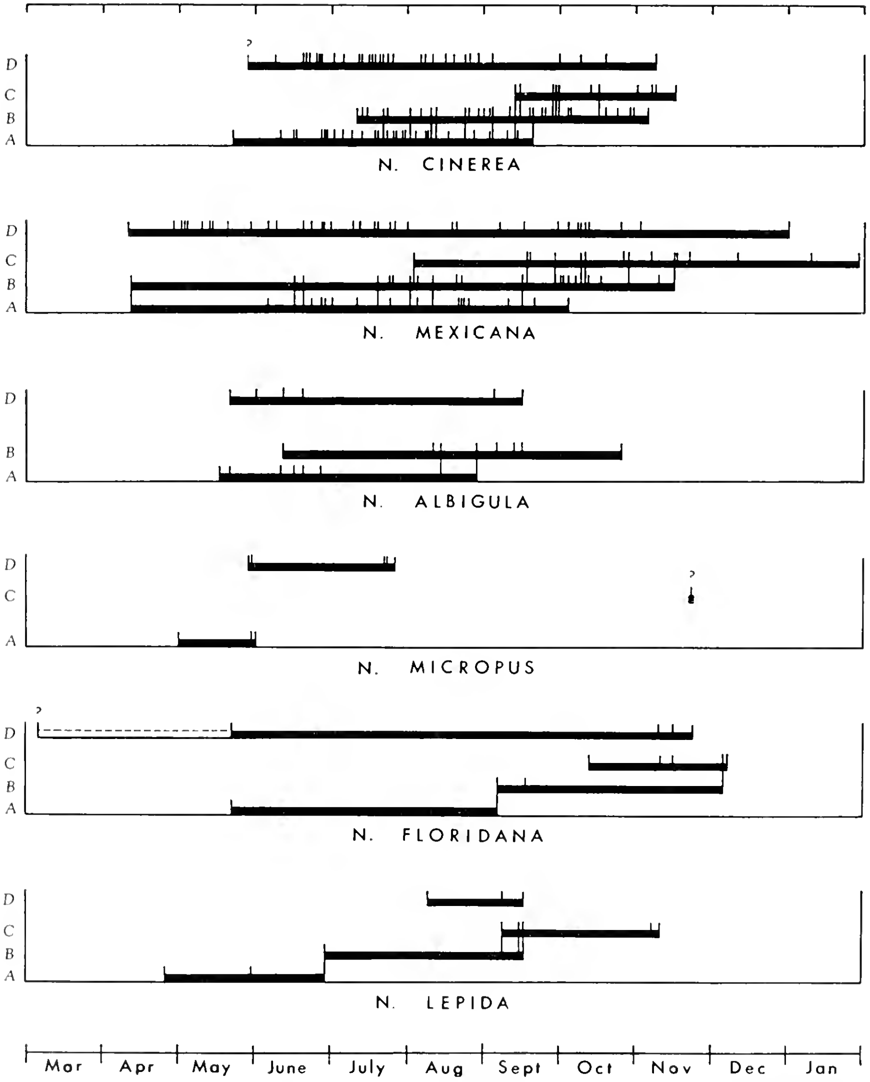


FIG. 2. Cup-shaped nest of *N. cinerea* composed of shredded bark of sagebrush, after removal from den 490717-5 beneath the rock, three miles north of Almont.

FIG. 1. Adult *N. cinerea orolestes* (Live No. 18 male) three miles north of Almont. Note rough, worn pelage and moderately bushy tail.

FIG. 2. Subadult *N. c. orolestes* (Live No. 17 female) three miles north of Almont. Note tufted tail with white fringe.

PLATE 22



Seasonal distribution of specimens in molt. Molts are as follows: A, postjuvenal molt; B, second molt; C, third molt; D, annual molt (all individuals more than one year old). Each short vertical line represents a specimen in molt. Each longer line joining two bars represents a specimen showing two molts at the same time.

Ixodidae

Dermacentor andersoni (larvae probably of this species). Live No. 1 (1 nymph), 480720-6 (3 nymphs), 480809-1 (1 larva and 1 nymph), 480811-1 (5 nymphs and 8 larvae), 480902-13 (3 larvae), 480903-1 (4 nymphs and 2 larvae), 490704-1 (5 nymphs and 4 larvae), 490705-2 (1 nymph and 1 larva), 490705-3 (3 nymphs and 11 larvae), 490724-3 (1 larva), 490724-6 (1 nymph and 4 larvae)
Ixodes woodi, 491018-1 (1 female and 1 nymph)

Argasidae

Ornithodorus sp., 480902-13 (1 larva)

Laelaptidae

Brevisterna utahensis, 490705-3
Euhaemogamasus ambulans, 491018-1
Haemolaelaps geomys, 480720-5
Haemolaelaps glasgowi, 490724-6

Macronyssidae

Hirstionyssus neotomae, Live No. 1, 480903-1

Erythraeidae

Balaustium sp. (probably a predator), 480720-5

Trombiculidae

Acomatacarus micheneri, 480902-13, 480903-1
Euschöngastia criceticola, 490705-3, 491018-1 and 2, 491101-1, 491116-2
Euschöngastia guntheri, 491018-1 and 2, 491116-2
Euschöngastia lacerta, 480720-3, 490724-6
Leeuwenhoekia americana, 470808-1, 491116-2
Trombicula (Eutrombicula) alfreddugesi, 480902-13
Trombicula (Neotrombicula) autumnalis, 491018-1 and 2
Trombicula (Neotrombicula) finleyi, 491018-1 and 2
Trombicula (Neotrombicula) harperi, 470808-1, 480731-1, 480810-2, 4 and 7, 490704-1, 490719-9
Trombicula (Neotrombicula) microti, 480810-2, 4 and 7

Haematopinidae

Neohaematopinus inornatus, Live No. 1, 480720-5, 480720-6, 480810-7, 490705-2, 490705-3, 490724-6

Cuterebridae

Cuterebra tenebrosa, Live No. 1, Live No. 9

Hystrichopsyllidae

Megarthroglossus sp., 491018-1, 491116-2
Phalacropsylla sp., 480810-2, 491018-1
Stenistomera alpina, 491116-2

Ceratophyllidae

Malaraeus sp., 480731-1, 480903-4, 490705-1, 490705-3
Monopsyllus wagneri, 490724-3
Orchopeas sexdentatus, Live No. 1, Live No. 2, 480720-5, 480720-6, 480731-1, 480809-1, 480810-2, 480810-4, 480811-1, 480902-13, 480903-1, 480903-4, 480909-1, 490705-1, 490705-3, 490719-9, 490724-3, 491018-1, 491101-1

Neotoma cinerea arizonae:

Ixodidae

Dermacentor andersoni, 490801-3 (3 nymphs and 1 larva), 490810-2 (2 larvae), 480909-1 (3 nymphs and 9 larvae), 491106-3 (1 larva)

Laelaptidae

Euhaemogamasus ambulans, 480909-1

Trombiculidae

Acomatacarus micheneri, 480829-1, 480909-1
Leeuwenhoekia americana, 491106-3
Euschöngastia criceticola, 491106-3
Euschöngastia lacerta, 490801-3
Euschöngastia finleyi, 491106-3
Trombicula (Eutrombicula) alfreddugesi, 490731-1, 490801-3
Trombicula potosina, 480829-1, 480909-1, 490731-1, 490801-3

Ceratophyllidae

Orchopeas sexdentatus, 480829-1, 480912-6, 490731-1, 490801-3

Neotoma cinerea rupicola:

Ixodidae

Ixodes spinipalpis, 500601-1 (1 nymph and 3 larvae), 500602-1 (2 nymphs and 5 larvae), 500602-2 (5 nymphs and 3 larvae)
Ixodes sp. near *I. ochotonae,* 500602-1 (1 nymph)

Laelaptidae

Brevisterna utahensis, 500602-1
Haemolaelaps glasgowi, 500602-1, 500602-2

Haematopinidae

Neohaematopinus inornatus, 500602-1

Cuterebridae

Cuterebra tenebrosa, 500601-1

Hystrichopsyllidae

Stenistomera alpina, 500602-2

Ceratophyllidae

Orchopeas sexdentatus, 500601-1, 500602-1, 500602-2

INJURIES AND DISEASE

A young adult male (ERW 1740) taken in December at Lake Moraine has suffered damage to the skull from some disease or injury from which the rat recovered. There is a hole opening into the braincase through the right posterior interorbital region, at the anterior junction of the right parietal and frontal. The aperture is bounded also by the tip of the squamosal and the dorsal branch of the alisphenoid. The aperture measures 4.6 mm long vertically and 2.7 mm wide on a horizontal, diagonal line. One can look through the orbit and hole into the cranium and out the foramen magnum. The entire bony margin of the hole has healed smoothly but has left four irregular nodular excrescences along the supraorbital margin, the outer one of which forms a recurved shelflike projection. On the anterior side of the interorbital constriction there is another irrregular, bony shelf projecting 1.0 mm over the orbit.

A second-year adult male (BSC 129814) from Gold Hill, 8 October 1903, has the ramus of the left mandible malformed by disease, which had affected the alveoli of the incisor and the third molar. The latter is reduced in size and separated from the second molar. The incisor is shorter than its mate and has a paler wavy enamel surface. The inner side of the ramus is noticeably swollen for 14 mm of its length. An interesting consequence of this ailment is that the upper incisors were used less than normal and grew to excessive length (10.5 mm on the enamel band, compared with 8.4 mm for a normal specimen).

An adult male (ERW 2098) from Grand Lake has the lower incisor broken off and decayed at the alveolus. Both upper incisors are longer than normal and worn medially to form an inverted V notch, the lateral edge of the left upper incisor extending 1.3 mm beyond the right incisor.

A live-trapped adult female (Live No. 5) 3 mi. north of Almont also had lost a lower incisor. When examined on 23 July 1948 she had a scab-covered wound not fully healed on the right side of the lip, below the missing tooth. The upper right incisor had already grown approximately a millimeter longer than the left and was beveled by wear on the medial side. On 13 August the scab was gone and the lip was fully healed.

An adult male (BSC 149105) from Ashbaugh's Ranch, Montezuma County, suffered some severe head injury. The maxillary branches of the zygomata are broken inward on each side of the skull and have healed. The rat's head seems to have been caught by some laterally crushing blow.

An old adult female *N. c. orolestes* (Live No. 1 or 490722-4) was so sickly and weak when live-trapped on 22 July 1949 that I killed her for internal examination. She was pregnant, lactating, and heavily infested with parasites. She was more than three years old, one of the oldest wood rats known to be in breeding condition, and one of the few *orolestes* known to have carried two litters in the same year.

When first caught on 19 July of the previous year, three miles north of

Almont, this rat weighed 218.3 grams. Her pelage was rough and without sign of molt. She had lost approximately half her tail and had a notch in her left ear. Her nipples were large and seemed to be drying up. She had at least 20 fleas and more than 100 lice, as well as many empty nit shells. When I held her up by the base of her tail, she whirled violently so that I had to let go to prevent her from twisting off the skin of her tail and leaving only the empty skin in my hand. She was released at the den of capture on the evening of 24 July and ran up a sandstone pillar out of sight.

When she was recaptured on 15 September she weighed 230.8 grams, a gain of 12.5 grams in eight weeks. Her nipples were small, indicating that she was no longer in breeding condition. A small warble was on her lower left jaw. A scar from a cut half an inch long crossed her right knee. New hair was beginning to grow in around the edge of the scar tissue, and she was in annual molt. I released her again where captured.

This rat was not caught again until 22 July 1949, when she looked sickly and lay inactive on the bottom of the trap. Her weight was only 216.3 grams. She had two large notches and a small one on her left ear and two small notches on her right ear. The scar on her right knee the preceding September had disappeared. She had innumerable lice and nits on most parts of the body and at least five fleas. Three larval ticks were attached to the pinnae, and a warble on the throat was ready to emerge. Her fur was thin and the skin dry and scaly, with scabs probably caused by the lice.

During the day she was in captivity she refused to eat or drink and became weaker. She could not stand up and seldom lifted her head. When disturbed she could move only by crawling. After killing her that evening I removed six tapeworms from the intestine and a cysticercus from the liver. She contained 4 embryos 8 mm long and was lactating. The small size of the embryos and the fact that her nipples were large and beginning to dry up indicate that she was carrying her second litter of the year, and that her first litter was probably being weaned. The crowns of her molars had been worn almost completely away, indicating that she was in her fourth year.

Neotoma mexicana Baird

Mexican wood rat

HABITAT

The Mexican wood rat occurs within a distinctly narrower range of climatic conditions than the bushy-tailed wood rat. These climatic conditions vary primarily with differences in elevation. The upper limit of the Mexican wood rat, between 7000 and 8500 feet in Colorado, depending on exposure, seems to be determined by temperature. The limit is in the upper part of the Transition Life-zone. Mexican wood rats in western Colorado are more abundant in the Upper Sonoran Life-zone than in the Transition. No parts of Colorado are too hot or too dry for the species, but in New Mexico and Arizona it never occurs so low as the Lower Sonoran Life-zone and is scarce even in the Upper Sonoran. The known distributions of *N. m. fallax, scopulorum,* and *inopinata* do not indicate any difference in climatic tolerances. These subspecies have nearly the same upper and lower extremes of elevation.

Most plant communities inhabited by Mexican wood rats are of open woodland or shrub type. The most widespread community favorable to *mexicana* in both western and eastern Colorado is the piñon—juniper woodland. In eastern Colorado the scrub oak—scattered ponderosa pine community is almost as important. In southeastern Colorado *N. m. scopulorum* lives in rocky situations bordering the short-grass plains. In the absence of rocks and associated shrubs the open short-grass plains do not provide shelter necessary for this species. Among the more common shrubs comprising the communities favorable for *mexicana* are scrub oak, mountain-mahogany, skunkbush, squaw currant, sagebrush, chokecherry, serviceberry, *Brickellia,* saltbush, *Ephedra,* and squaw-apple.

The numbers of dens examined in each kind of plant community and in each life zone are presented in Table 13 for each subspecies.

A wide variety of rocky situations are selected by *N. m. mexicana* for shelter. Occasionally a rat builds its den in an abandoned cabin,

TABLE 13.—LIFE-ZONES AND PLANT COMMUNITIES OF N. MEXICANA

LIFE-ZONES AND COMMUNITIES	Number of dens		
	N. m. fallax	*N. m. scopulorum*	*N. m. inopinata*
Transition zone:			
Open ponderosa pine forest	1		
Ponderosa pine—scrub oak			1
Scrub oak—scattered pines	5		2
Mountain-mahogany—scattered ponderosa pine	1		
Upper Sonoran zone:			
Piñon—mountain-mahogany			1
edge Scrub oak and Piñon—juniper			2
Piñon—juniper	2		16
Juniper—sagebrush			9
edge Sagebrush and Mixed shrub			3
edge Scrub oak—mixed shrub and Willow—alder			1
edge Scrub oak—mixed shrub and Cottonwood			2
Short-grass—scattered shrubs		1	
Yucca—short-grass		4	
Totals	9	5	37

mill, or other man-made structure. The type specimen of *N. fallax* came from an old mill. Except for such man-made habitats, *mexicana* rarely, if ever, occurs away from rock shelter of some kind. Caves and mine tunnels are sometimes occupied, although not so commonly as by *cinerea.* Boulders and large fallen blocks of sandstone seem to be the kinds of shelter most used by *mexicana.* Horizontal crevices under rock ledges are also frequently occupied. The Mexican wood rats are most numerous on rocky canyon sides or mountainsides or along rimrock outcrops, because their preferred kinds of rock shelter are here most abundant. Many kinds of rocky habitats, such as vertical and diagonal crevices in cliffs, and

TABLE 14.—SHELTER AND TOPOGRAPHY OF N. MEXICANA

SHELTER	Topography and number of dens								
	Cliff above steep slope	Cliff by valley bottom	Rimrock outcrop above steep slope	Rimrock above moderate slope	Steep mountainside or canyon side	Base of steep slope	Moderate rocky slope	Sandstone hogback	Totals
Vertical rock crevices	....	....	....	....	1	....	....	....	1
Vertical cleft through sandstone block	....	....	....	....	....	1′	....	....	1
Vertical and diagonal joints in granite	....	....	....	....	1′	....	....	....	1
Vertical and horizontal crevices	1	1″	....	....	2	....	....	....	4
Cave and vertical crevices	1	....	....	....	....	....	....	....	1
Low cave and horizontal cleft behind rocks	....	1″	....	....	....	....	....	....	1
Diagonal crevices in overhanging cliff	....	1	....	....	....	....	....	....	1
Horizontal and diagonal crevices	1	....	....	....	....	....	....	....	1
Horizontal crevices	1	....	1	....	1	....	1′	....	4
Crevices in outcrop and between rock blocks	....	....	....	1′	....	....	1′ 1″	1′	4
Loose sandstone block beneath overhang	1	1	....	....	2	....	....	....	4
Several boulders	1	1″ 1	2	....	3	1′	1′ 1″	....	11
Under and between 2 big rock blocks	....	....	4	....	....	....	....	1	5
Big sandstone block	....	2	2	....	1	2	1′ 3	....	11
Sandstone block and house in skunkbush	....	1	....	....	....	....	....	....	1
Totals	6	9	9	1	11	4	9	2	51

crevices in sandstone hogbacks, occasionally provide suitable shelter. Stick houses have been found only where some rock shelter was already present over which the pile of sticks and other debris could be heaped.

The numbers of dens examined in each kind of shelter and in each kind of topography are presented in Table 14. Prime digits refer to *N. m. fallax.* Double prime digits refer to *N. m. scopulorum.* Plain digits refer to *N. m. inopinata.*

Dens of the Mexican wood rat were numerous at Daniels Park, 6400 feet, 7 miles north and 4 miles west of Castle Rock in 1948. The top of the mesa was mostly grassy with scattered ponderosa pines and shrubs. Below the rim the slopes were moderately steep and densely grown to scrub oak, with scattered ponderosa pines and Rocky Mountain junipers. Other characteristic plants of the slopes were thimbleberry, squaw currant, mountain-mahogany, and Oregon grape. Most of the dens seen were below the rim of the mesa overlooking the valley westward. They were in crevices in and under the coarse sandstone rim, which was 6 to 10 feet high. Other dens were under blocks of sandstone that had broken off the rim and come to rest on the slope. The pattern of distribution was essentially linear, following the rim.

Two typical dens in the piñon—juniper zone were studied 18 miles south and 7 miles west of Colorado Springs at 6200 feet elevation. They were at the foot of a low rounded hill on the east side of a broad grassy valley. Sandstone boulders lay scattered over the hillside, which was fairly well shaded with piñons and one-seed junipers. Tree cacti were numerous on the dry stony soil and two kinds of prickly pears (*O. polyacantha* and *O. humifusa*) were present. Skunkbush, chokecherry, snowberry, soapweed, and *Ribes* also grew on the hillside. At the edge of the highway that skirted the base of the hill, grew numerous weeds and forbs, including sweet clover, *Lepidium, Tragopogon,* and false ragweed. One of the two wood rat dens was in a vertical crack through a big sandstone block. The other den was in joints and spaces under smaller loose rocks and overlain with a thin layer of sticks and piñon cones.

Mexican wood rats of the subspecies *scopulorum* live in the rocky canyons and gulches that cut through the High Plains in southeastern Colorado. Specimens were trapped and dens were examined in the rock cliffs that border the valley below the dam of Two Buttes reservoir. Plains cottonwoods grew by the creek, and the valley bottom was covered with grasses, soapweed (*Yucca glauca),* and low shrubs. A line of red cliffs of Dakota sandstone perhaps 40 feet high bordered the valley bottom on the north side. Similar but less continuous cliffs bordered the south side. Soapweed, sand sage, *Brickellia* and scattered skunkbush grew among the rocks at the base of the cliff on the north side. On the south side in addition to these plants dense thickets of chokecherry lined the base of the cliff. A den was situated at the ground level in a low cave under the cliff, behind fallen blocks. Another was in horizontal clefts and nearly vertical cracks in the base of the cliff. A third den was in a small cave in the upper part of the north-facing cliff. This cave was said to have been a "wildcat" den the previous year.

Dens of *scopulorum* were also studied high on the rocky slopes of Two Buttes. One was on the northwest-facing slopes under a pile of boulders among which a low dense thicket of skunkbush was growing. Another was in joints in the bedrock and under a loose block on the east-facing slope. Skunkbush was the most abundant shrub on the upper slopes of Two Buttes. Other shrubs present were gray saltbush, soapweed, and a species of sage. *N. albigula* lived among rocks on the lower slopes of Two Buttes (see p. 462).

The habitat occurrence of *scopulorum,* as well as that of *N. a warreni,* in the Purgatoire Valley is described in the habitat section under *Neotoma albigula* (see p. 451). The habitat of *scopulorum* at Regnier is shown in Pl. 24, Fig. 2 (see also the habitat section under *N. micropus,* p. 488).

On the south side of the San Miguel Valley, one mile east of Naturita, Mexican wood rats of the subspecies *inopinata* live among rocks and cliffs on the steep slope. The hillside supports an open stand of piñons and junipers. Scattered piñons and junipers grow on the upland approximately 100 to 200 feet above the valley bottom. Common shrubs among the rocks are serviceberry, skunkbush, rabbitbrush, sagebrush, and gray saltbush. Mormon tea and hunger cactus are less numerous. The rocks forming the upland, cliffs, and talus boulders are of white and tan sandstone of variable texture, pitted and fissured by erosion. They look like the Dakota sandstone and have been mapped as that (U. S. Geol. Surv., 1935). At one end of the cliff four Mexican wood rats were trapped on two nights in a cave that narrowed toward the rear and then opened upward into a vertical cleft. The den is described on page 420. Another den farther east was behind a loose block beneath the overhanging cliff and in a vertical crevice above.

A third den (490626-4) at the same locality was higher up the hillside in a rocky draw that led out onto the upland. Shelter was provided by a huge block of the sandstone rim that had broken off and dropped a few feet down the slope. Beneath the block were two separate middens made by different species of wood rats, *N. mexicana* and *N. albigula.* This den is described below on p. 421.

A habitat in which both *N. m. inopinata* and *N. c. arizonae* live side-by-side is the north rim of Cahone Canyon, described under the account of *N. cinerea* (see p. 362).

Habitats occupied by *inopinata* and *N. a. brevicauda* near Gateway are described under the account of *N. albigula* (see p. 450).

N. m. inopinata lives in the same habitat with *N. albigula laplataensis* at Bondad which is the type locality of the latter. In 1949 *inopinata* was the more abundant of the two kinds. They lived in rock dens along low sandstone cliffs and outcrops forming the banks of the Animas River, whose course is incised some 30 feet below the bottom of the valley. Sagebrush, *Opuntia rhodantha,* hairy goldaster and other low shrubs, forbs, and grasses covered the gravelly valley-bottom extending back from the sandstone rimrock. Along the rim and below it on the sandy soil among fallen rocks there were Rocky Mountain junipers, scrub oak, mountain-mahogany, skunkbush, chokecherry, golden currant, serviceberry, *Fendlera rupicola,* paloblanco, rabbitbrush, prickly pears and numerous forbs and grasses. A few cottonwoods and willows grew close to the water's edge at scattered points along the river.

Dens of Mexican wood rats were under and between the large fallen blocks, in horizontal and vertical crevices in the standing rock-face, and under smaller boulders resting on the bedrock outcrop. The only den studied of the white-throated wood rat was under low boulders resting together atop the sandstone outcrop. It differed from the other dens in having a midden of solidly enmeshed cactus spines. At one of the larger dens under large blocks almost against the rimrock I caught a *mexicana* and an *albigula* under opposite sides of the same block (see p. 423).

The valley of the Florida River, two miles northeast of Bondad, is much narrower than the Animas Valley and has not been secondarily incised. The shallow Florida River flows at the base of a steep mountainside on the east side of the river, and large sandstone talus blocks from low cliffs and outcrops above have come to rest in the river bed. On the west side a low cliff rises directly from the valley bottom. Farther north the valley widens and the mountainsides rise more gradually from the valley. Den sites and vegetation are essentially of the same kinds as described at Bondad, except for the narrow flood bottom of the Florida River on which grow narrowleaf and Rio Grande cottonwoods, alder, and willow. Higher on the mountainsides junipers and piñons are dominant. Dens of both *mexicana* and *albigula* were numerous, the former being more abundant in large clefts of the cliffs and the latter more numerous in drier situations under smaller ledges or fallen blocks. A few large unusual dens of *mexicana* on the flood bottom were built of heaps of food litter against boulders and crevices. For a description of one of these see page 419.

Dens of *N. mexicana* and *N. albigula* were numerous in Mancos Canyon, as described on page 450, and in the valley of Cherry Creek, as described on page 451.

DENS

The Mexican wood rat has the weakest collecting instinct of any species of wood rat in Colorado and builds a house of sticks or other debris only where a natural rock shelter is already present. Most of the better rock dens contain few, if any, large sticks or bones, as are commonly gathered by the bushy-tailed wood rat. The middens of such rock dens contain little other than rat feces and food litter. Some dens of *mexicana* contain a fair amount of small sticks and other miscellaneous objects that partly close crevices and exposed spaces under rocks. Dry joints of cactus and spines are ordinarily scarce, probably because so little cactus is brought in for food. Rarely a large pile or house of sticks is built over a rock crevice or against a block. Such a house may be mostly an accumulation of shrub twigs and leaf cuttings gathered for food. Although *mexicana* seldom gathers large amounts of strictly non-edible building materials, in the autumn it gathers and stores large quantities of food, as is described in the section on food below.

Dens of *mexicana* occur in a wide variety of rocky situations including both vertical and horizontal crevices, but perhaps more commonly in low horizontal spaces under large rock blocks and boulders. Crevices and low caves in bases of rock outcrops are

TABLE 15.—MATERIALS ACCUMULATED AT DENS OF N. MEXICANA.

MATERIALS	Number of dens			Totals
	N. m. fallax	*N. m. scopulorum*	*N. m. inopinata*	
sticks	8	3	33	44
scrub oak	3		4	
sagebrush	1		6	
juniper			6	
piñon	2		2	
other pine	1		1	
mountain-mahogany	2			
cottonwood			2	
skunkbush		1		
rabbitbrush			1	
snowberry			1	
greasewood			1	
unidentified	2	2	22	
bones	2	4	16	22
pine cones	6		7	13
cactus joints and dry fruits	4		8	12
Opuntia (Platyopuntia)	2		6	
O. davisii			3	
O. arborescens	2			
Mammillaria vivipara			1	
livestock dung	3	2	4	9
carnivore scats	1		7	8
bark			8	8
juniper			4	
pine			2	
scrub oak			2	
cottonwood			1	
small stones		1	7	8
yucca blades and stalks		3	3	6
dry weed stalks		2		2

Each of the following items was present at one den of the subspecies: *fallax:* Douglas-fir cones, piece of dry skin of cottontail, pieces of paper plates, Roman candle stick (burned), bottle caps; *scopulorum:* dry thistle leaf, owl pellet, paper, white handkerchief; *inopinata;* cockleburs, dry rosette of mullein, dry leaf of Oregon grape, wingtip of bird, feathers, jackrabbit foot, fish fin, piece of chewed cloth, potsherd.

also frequently used. Over a large part of the range of *mexicana* at least one other kind of wood rat may occur at the same locality, and often among the same rocks. When *cinerea* is present it usually prefers higher vertical clefts in cliffs and *mexicana* occupies the lower ledges and spaces under talus blocks. But if *cinerea* is not present, *mexicana* sometimes occupies vertical clefts and high caves that otherwise would be used by *cinerea*. When *mexicana* and *albigula* live among the same rocks there is no distinction between the kinds of rock shelter selected by each. Occasionally the same large block shelters dens of both species, which, however, are probably not occupied simultaneously. *N. mexicana,* like most wood rats, sometimes builds its nest in an abandoned cabin, mill, or other building made by man.

Nests of *mexicana* were seldom obtainable, because the dens of this species were all in rock crevices or under some kind of rock shelter. Only six nests were examined. In addition, as many more dens, at which no nest was found, had some scattered nesting material mixed in the middens. From this evidence it seems that shredded juniper bark is the most commonly used material. Occasionally a nest is made of shredded sagebrush bark or of fine yucca fibers. Some nests are cup-shaped and some are ball-shaped. None of these features are at all distinctive from those of other kinds of wood rats in Colorado.

An outcrop of sandstone forming a hogback ridge at the edge of the eastern foothills provides good shelter for dens of the Mexican wood rat. Such a den was examined one and a half miles northwest of Golden, 6200 feet elevation, where an adult *N. m. fallax* (480708-1) was trapped on 8 July 1948. The common shrubs were Rocky Mountain juniper, mountain-mahogany, squaw currant, and a species of *Artemisia.* Small ponderosa pines were widely scattered along the hogback. The den was in diagonal crevices between the bedrock and a loose block of sandstone. A deep midden of food litter and rat feces filled the main crevice. Approximately 90 percent of the accumulated material consisted of twigs and dry leaves of mountain-mahogany, mostly as food litter. There were also a few pine cones and needles; twigs and sticks of pine, juniper, and sage; horse and cow dung; and a dry joint of prickly pear cactus. The nearest bush, a squaw currant, had been but little disturbed, although mountain-mahogany farther away had been pruned.

A den higher in the mountains, 2 miles east and 1 mile south of Gold Hill, at 7100 feet, used diagonal and vertical joints in a massive outcrop of granite on a steep rocky mountainside. The crevice mainly used was diagonal and 4 to 5 inches wide. An adult male (491121-1) was trapped at this den on 21 November 1949. The slope was sunny and supported an open forest of ponderosa pines with scattered Rocky Mountain junipers and a few Douglas-firs. Shrubs growing within 100 feet of the den were squaw currant, *Yucca glauca, Ceanothus fendleri,* thimbleberry, *Jamesia americana* and *Opuntia polyacantha.* There was not much den material in or about the crevices, only a few small sticks, carnivore scats, Douglas-fir cones, dry cactus joints, and food litter consisting mainly of shrub twigs and cuttings. Low bushes of *Ceanothus* and stalks of sunflower (*Helianthus rigidus*) growing close to the den had been much pruned.

A den under an outcrop of horizontal sandstone rimrock was examined at Daniels Park, 7 miles north and 4 miles west of Castle Rock. A subadult female (480804-2) was trapped at this den on 4 August 1948. The habitat is described on page 411. The den occupied a horizontal space beneath a projecting rock overhang. A small rock ledge a foot above the soil and far back under the overhang was much used as a resting place or lookout post by the rat, as indicated by a black fecal deposit as much as an inch thick in spots. The den contained little material—only a few sticks and pine cones.

Another rock den at Daniels Park was noteworthy for the abundance of building material piled in the clefts. On 4 August 1948 a subadult female (480804-6) was taken at this den, which was situated in clefts in the face of the rimrock and between blocks remaining almost in place. The main vertical cleft separating a block from the outcrop contained a mass of sticks that at one open end of the crevice was heaped up into a pile. There were approximately two bushels of sticks of scrub oak and mountain-mahogany, pine cones, horse dung, a bone (radius of a large dog), and a Roman candle stick that had probably been burned the preceding Fourth of July on the picnic ground above the rim. Judging from the large size of the den, its ancient appearance, and the presence of spider webs on the sticks at one end of the cleft, the den probably had a long history and had only recently been occupied by the young rat.

A large block of sandstone lying by a roadside ditch at the foot of a steep hillside contained a den in a vertical crack running through the block. The habitat, 18 miles south and 7 miles west of Colorado Springs, is described on page 411. An adult female (480916-2) was trapped there on 16 September 1948. The rock seemed to be solidly imbedded in the ground, and there was probably no natural space under the block that could be used by the rat as part of its den.

The dimensions of the whole block were approximately 22 feet in length, 13 feet in height above the ditch, and 4 feet in height above the upper side of the bank. The den crevice varied from 2 to 6 inches in width, and a large part of its depth was crammed with den material and food litter. The former was composed mostly of piñon sticks and cones, the most abundant transportable debris available to the rat. There were also green and dried joints of tree cactus, dry cow dung, a piece of dry cottontail skin and the dried remains of a wood rat. More than a gallon of cuttings of skunkbush were stored in the crack. A cup-shaped nest of shredded bark of the one-seed juniper was lodged in the wide part of the crevice six feet above the ditch and behind the pile of stored food.

An exceptionally well sheltered den was under a pile of talus boulders on a steep rocky hillside near the top of Two Buttes. Not only was a great deal of space sheltered by the loose rocks but the openings between the rocks were shielded by a screen of skunkbushes growing between the boulders and forming a low thicket 10 yards long and 7 yards wide. An adult male *N. m. scopulorum* (500509-9) was trapped under a rock on 9 May 1950. As might be expected, not much shelter material had been brought into this den. There were a few sticks of skunkbush, dry weed stalks, small stones; scraps of paper, and a white handkerchief.

There was a considerable quantity of food litter and rat pellets on the ground under and between rocks. At least three gallons of mixed leafy cuttings were stored under the rocks. Skunkbush provided about 50 percent of the food. Since the screening thicket, having a northwest exposure, was in flower but not yet in leaf, the cuttings must have been gathered the preceding year. The skunkbushes had been pruned and the bark gnawed by the wood rat.

A low cave at the base of a sandstone cliff was used as a den in the valley below Two Buttes Reservoir. The topography and vegetation there, and of the surrounding country in the vicinity of Two Buttes, is described in the section on habitats (page 411). A pregnant female (500509-1) was trapped in the cave on 9 May 1950. The floor of the cave was covered by a shallow midden of food litter and rat pellets (see Pl. 26, Fig. 2). The scanty material other than food litter consisted of a few sticks and driftwood, dry yucca blades, a piece of dry cow dung, and a few bones (*Mephitis, Cratogeomys, Cynomys, Dipodomys, Bubo virginianus,* and chicken). The cave may have been used also by a skunk. On a ledge near the top of the cliff a great horned owl had her nest containing two large young.

At the base of the same cliff another den of *mexicana* occupied much less space in horizontal and nearly vertical crevices. The crevice along the base of the cliff was 3 to 12 inches high and 16 feet long. It contained no sticks, only midden material, yucca blades, an owl pellet, a few small bones, and a dried carcass of a Mexican wood rat. A large adult male (500510-1) was trapped at this den on 10 May 1950.

A fine den of *N. m. inopinata* was sheltered by a large sandstone block 2 miles west and 1 mile south of Chromo, 7200 feet elevation. On 16 November 1949 an adult female (491116-3) was trapped there. The block was on the moderate lower slope of the Navajo River Valley where it had fallen from the cliffs forming the north wall of the valley. Scrub oak was the dominant vegetation, with scattered ponderosa pines and Rocky Mountain junipers. Other shrubs on the moderate slope were skunkbush, rose, and Fendler's barberry.

The block, approximately 20 feet long and 10 feet high, had been split through one end by a diagonal cleft 8 to 12 inches wide and 10 feet long. This cleft and inaccessible spaces under the rock were used by the rat. A moderate number of small sticks, long twigs, and slabs of bark of scrub oak had been accumulated in the diagonal crevice and were mixed with fallen leaves and other detritus. There were a few sticks up to 30 inches in length, and one carnivore scat. On top of this debris and partly mixed with it there was a storage supply of oak cuttings amounting to at least five bushels in a layer from 1 to 2½ feet deep. Scattered cuttings of pine and juniper needles were mixed with the dry light green to brownish cuttings of oak foliage. The supply was packed so tightly into the crevice that it is improbable this could have been packed by the wood rat with cuttings already dried elsewhere. The leaves seemed to have been cut and stuffed into the cleft while fresh and then dried in place. The large secure shelter and wealth of stored food at this den should have given this rat a good chance of surviving the winter.

One of the smallest dens studied was under two boulders, the smaller of which rested on the other on a steep slope covered with gravel and boulders one mile southwest of Gateway. A large adult male (490819-1) was trapped at this den on 19 August 1949. The topography and vegetation of the area are described in the habitat section of *N. albigula* on pages 449 and 450. The larger boulder was 7 feet long and 30 inches high at the lower side, which was partly screened by a juniper. There were no sticks or other building materials, only food litter and rat pellets. Fresh food litter, mostly of juniper cuttings and nutlets, was on top of the big rock, some under the smaller rock and some in the open. A ball-shaped nest of juniper bark was under the lower boulder.

A den containing a massive cemented fecal deposit was in a 25 foot section of rimrock that bordered a low broad creek valley seven and one half miles west of Montrose at 6000 feet elevation. The dominant vegetation was sagebrush with scattered Utah junipers. The section of rimrock harboring the den was broken apart in several places by wide vertical cracks and narrow crevices in the bedding planes. The large solid fecal deposit was in the largest vertical cleft, which contained also a few slender sticks, a deer mandible, a loose midden of food litter and rat pellets, and two gallons of stored food cuttings.

A large den 3 miles west and 2 miles south of Cahone was in a vertical cleft between two huge blocks of sandstone that had broken loose from the rim outcrop of Cahone Canyon. The cleft was crammed to a height of approximately five feet with many sticks. Both blocks rested on a rocky surface so that there was a wide area under them several inches high that was used as den living space by the rat. Large fecal deposits had accumulated under the outer block.

Among the sticks in the cleft were a cervical vertebra and the pubis of a Ute Indian who had been buried in a wide vertical cleft 50 yards west northwest of the den many years before. Dr. Carlisle Smith judged the bones to be those of a child 10 to 12 years old. Other materials gathered by the rat were a much gnawed deer scapula, two cottontail bones, many flat stones, and a mass of matted shredded juniper bark (old nesting material). The rat trapped at this den on 5 August 1949 was a young adult male (490805-2). The habitat is described on page 362.

One of the most substantial and well protected dens that I have seen was on a steep rocky canyon side 6½ miles east and 2 miles south of Cahone. On 19 August 1949 an adult male *inopinata* (490819-1) was trapped at the den. An unusually large mass of sticks had been piled into a trenchlike space behind a long fallen piece of sandstone outcrop (see Pl. 27, Figs. 1, 2). The canyon side supported an open piñon—juniper woodland with numerous shrubs, of which serviceberry, rabbitbrush, mountain-mahogany, and *Yucca baccata* were the most common. Bunchball cactus and prickly pears (*O. phaeacantha*) also grew within 100 feet of the den.

The detached block of sandstone was 32 feet long and 8 feet wide. The overhanging outcrop from beneath which the block had fallen projected nine feet from the bedrock behind the heap of sticks. Before the heap was dismantled, its entire top appeared to be flush with the ceiling formed by the overhang. The sides of the pile dropped off steeply to the bottom of the "trench". The pile measured 78 inches in length, 64 inches in width, and 35 inches in depth. The area of the top seemingly in contact with the rock ceiling was 5 to 5½ feet long and 4 feet wide. The total volume of the heap of sticks was estimated to be between 50 and 60 cubic feet.

Removal of the outer sticks at one side of the pile revealed that much of the upper part of the pile was occupied by living spaces approximately three inches high, roofed only by the rock overhang, and walled around by sticks, yucca blades, and stones. In these chambers there were 1 to 2 quarts of loosely stored green foliage cuttings consisting mostly of mountain-mahogany, with less of juniper and piñon, and only a little of serviceberry. Roughly a foot lower in the stick pile there was another level of passageways, some of which opened to the outside at each end, that is, within the trench. A nest of juniper bark was found in the den.

In location, the stick pile was part of a rock den, the materials serving to fill partially the spaces between rocks and thus provide better protection. But structurally the pile was also a house, for it contained living spaces entirely enclosed within the mass of material accumulated by the wood rat.

As dismantling of the house progressed, the task of removing the materials from the confined space of the "trench" became more difficult and time-consuming. Consequently the bottom half of the heap, which showed no significant new materials or features, was not fully excavated. The most abundant materials were sticks of piñon and Utah juniper. Dry yellow leaf-blades of *Yucca baccata* were also numerous. Other occasional items were bark and cones of piñon, bark of juniper, flakes of sandstone, dry joints of *Opuntia phaeacantha,* carnivore scats, feathers, and bones (cottontail, deer, beaver, striped skunk, rock squirrel, Mexican wood rat, short-eared owl, and a snake). The abundance of large items was highly unusual for the Mexican wood rat, which ordinarily carries in few sticks larger than a pencil. At this den the largest pieces, of 3 kinds, were a stick 28½ inches long, a slender branch of rabbitbrush 31½ inches long, and a dry blade of *Yucca baccata* 22½ inches long. Although cactus spines, dropped as food litter, did not compare in numbers with those found at most dens of *N. albigula,* the spines were abundant for *mexicana* and required much caution in working on the den. Spines of the brittle cactus were the most numerous kind.

An extraordinary den, for the Mexican wood rat, was studied in the Florida Valley, two miles northeast of Bondad. A large peaked house had been built in a dense clump of skunkbush and close against the south side of a high boulder at the edge of the valley bottom. The top of the boulder was more than 12 feet above the foot of the slope where it rested. An adult female (491024-4) was trapped at this den on 24 October 1949.

Although the house superficially resembled one of *Neotoma floridana* or *N. fuscipes,* it differed both in materials and construction. It was a great accumulated mass of food twigs and contained no sticks larger than approximately half an inch in diameter, in spite of the availability of sticks from many kinds of trees and shrubs. Most of the twigs were of skunkbush from which the leaves had been eaten. Much long dry grass lay on the top and upper sides of the house and was mixed with the twigs. Scarce items of more conventional house materials were pieces of cottonwood bark up to ten inches in length, a few stones one and one half inches in diameter, a few deer or sheep bones, a few dry prickly pear joints, and a carnivore scat.

The house was 21 inches high above the base on the uphill side and 65 inches high above the base on the downhill side. The base extended 60 inches parallel to the side of the boulder and 33 inches out from the boulder. There were 4 entrances on the uphill side at two levels and 8 on the downhill side at 5 levels. The lower entrances were behind a screen of drooping skunkbush branches. There was no midden of any size in or outside of any entrance, or elsewhere around the house or boulder; but the innermost spaces of the house were largely filled with midden, a mixture of food litter and fecal pellets. The mass of food litter forming the house was accumulated around the densely crowded basal stems and branches of skunkbush which both supported and strengthened it. Passages were mostly under branches or stems where spaces were left by the haphazard piling up of the twigs. In dismantling the pile no large chambers were found in the house, and no functional pattern of passages was discerned. The inner spaces of the pile were filled almost solidly with midden materials, but the outer spaces were stuffed with recently stored food cuttings.

Because of the difficulty of chopping out the brush, only the top 20 inches of the house were fully removed, and the lower east side partially. No nest was found, nor any burrow. Because of the absence of chambers and the accumulation of midden in the base of the pile, it is presumed that the nest and inner recesses of the den were under the boulder. Such a location would be typical for the Mexican wood rat, had a den existed under the rock prior to the building of the house. Even after the accumulation of the mass of material, the house seemed to be more an accessory place for storing food and dumping refuse than a main sheltered living space.

An old den was in a cavelike room under an overhanging sandstone outcrop 3 miles west and 1 mile south of Durango. The outcrop stood 15 feet high and projected 10 feet horizontally over the room, which had been formed by the fracture and fall of a large mass of rocks from the base of the outcrop. Several large blocks partially blocked the entrance and a mass of rock waste covered the floor. The steep southeast-facing slope below was partly covered with shrubs, predominantly scrub oak. On the high parts of the slope there were scattered piñons, ponderosa pines, Douglas-firs, and Rocky Mountain junipers. The rat trapped alive on 31 August 1949 at this den was released, and the den was numbered 490831-1.

Under a long flat fallen block beneath the cavelike overhang there was a large midden of rat pellets and food litter, mostly scrub oak twigs. There were a number of oak, pine, and other sticks, and three bones scattered on the midden and elsewhere under the overhang; but the quantity of such den materials was slight in proportion to the volume of midden materials. A fecal deposit six feet long had accumulated on top of the flat block. A nearly vertical cleft behind another block of sandstone was filled with a big midden and fecal deposit. This den was probably one of the most desirable and continually occupied in the area because of the large over-all shelter and the innumerable inner recesses.

A den one mile east of Naturita was in a kind of rock shelter usually occupied by the bushy-tailed wood rat, a cave large enough to walk into, with a narrow vertical crevice leading upward from the rear to the ground surface. Four Mexican wood rats were taken in two traps set on two nights, from 25 to 27 June 1949, in this cave. A pair of adults (490626-8 ♂ and 490626-9 ♀) were caught the first night and two males, subadult and adult (490627-5 and 490627-6), the second night.

The cave was in soft white sandstone of the Dakota formation on the south side of the San Miguel Valley. A clump of serviceberry growing by the mouth of the cave had been heavily pruned. The habitat is described in more detail on page 412.

The floor of the cave was covered with a bed of wood rat pellets and food litter. On rough projections and narrow shelves high up on the walls of the cave there were solid masses of blackish fecal deposits like those nearly always associated with rock dens of *N. cinerea*. The cave had obviously been occupied for a great many years. Two wings of the cave both contained masses of midden continuous with that in the main part of the cave. No nest was seen and it could not be determined whether the individual rats had two or more separate dens within the cave. The upper part of the vertical crevice through the roof of the cave had been solidly filled with rocks and dirt from the ground above, probably by runoff, not wood rats.

The identity of the occupant of the cave should have been revealed to me upon first examination by a single distinctive characteristic, namely, that sticks and other materials larger than food litter were extremely scarce for a mass of rat feces and litter of this size. Such a den occupied by *cinerea* would almost always contain many large sticks and bones. The only materials in this cave other than food litter and feces were extremely few juniper sticks, a few small bones (cottontail, muskrat, beaver, and Mexican wood rat), a few porcupine quills, and some shredded juniper bark.

A few dens at which *N. mexicana* were caught gave evidence of some association with *N. albigula.* In one instance separate middens of both species were under the same sandstone block. In two other cases, old dens of *albigula* had been taken over by *mexicana.* At another den both species were trapped on the same night although the den seemed to have been occupied only by *mexicana.* These dens are described in the following paragraphs.

Distinct middens of *N. mexicana* and N. *albigula* under the same large block were not far from the cave den described above, one mile east of Naturita. The block was a piece of sandstone rimrock more than 20 feet long and 6 feet high that had broken loose and slid a few feet down into a shallow rocky draw. There was ample sheltered space under the block for two dens, but if two independent dens really existed simultaneously, the living spaces were almost certainly interconnected, if not completely continuous from one end of the block to the other. More likely, the two kinds of wood rats did not live there at the same time. In any case, a subadult female *N. mexicana* (490626-4) was trapped under the upper side of the rock on the more extensive midden containing mixed food litter and fecal pellets. Not a single cactus needle was found in this midden by raking and sifting it through my fingers. Only two and a half feet away under the lower end of the rock was a midden composed almost entirely of cactus areoles and rat pellets. A trap set on the spiny midden was untouched. Spider webs under the edge of the rock and the lack of fresh litter on the cactus midden showed that this midden was no longer in use by the white-throated wood rat that made it. However, fairly recent piñon cuttings lay around the front of the den and on a raised lookout perch. The food litter in the spineless midden of *mexicana* consisted mostly of cuttings and needles of piñon, with a few piñon shells, cuttings of juniper and serviceberry, and flower stalks of sagebrush. Some of this litter was fresh. There were a few sticks on the *mexicana* midden and a few small bones on and in front of the *albigula* midden.

Traps were set on two occasions at many dens in Dolores Canyon, 8 miles north and 3 miles east of Egnar, 5800 feet elevation. Although some of the dens had large cactus middens that could only have been made by *albigula,* no wood rat of this species was obtained. However, two young adult *mexicana* of the year (490821-1 and 490821-2) were trapped at two dens with cactus middens on 21 August 1949. These middens were composed of old dry brown areoles of *Opuntia hystricina.* None of the areoles looked recent. But each den had a few recent (green but dry) cuttings of other plants probably gathered by the *mexicana*.

Both dens were under large sandstone blocks at the base of the steep canyon side on the east side of the Dolores River. The steep rocky slope was dotted with piñons, Utah junipers, sagebrush, and shadscale. The most common kind of cactus was *Opuntia hystricina,* which provided nearly all the spines composing the middens. *Echinocereus coccineus* and *Echinocactus whipplei* were, respectively, less and least numerous; and a few areoles of the latter were mixed with those of *O. hystricina* in each of the two middens.

Den 490821-2 had good shelter and a large old midden but was in poor condition; it seemed to have been unused for a long time prior to the recent occupancy by the young Mexican wood rat. A remarkable feature of this midden was its stratification. There were three superimposed layers of midden, each composed predominantly of one food material. The basal layer, three inches deep in the middle, was formed almost entirely of *Opuntia* areoles. Above that was a layer of piñon needles and cuttings two and one half inches deep. On top was another layer of *Opuntia* areoles five and one half inches deep and completely covering the piñon layer. Each layer extended over most of the area of the midden. The piñon layer was at least three feet wide along the exposed front where I excavated the midden.

Two possible explanations come to mind. The stratification may have resulted from seasonal activities, the bed of piñon being a winter food store gathered the previous fall. A large proportion of the needles seemed to have been uneaten, and the quantity could have been gathered in a single season. However, stored food is almost never spread evenly over an entire midden. It usually is stuffed together in one part of a large crevice or storage space, if the amount is not enough to fill the space. Another difficulty with the storage explanation is that piñon needles were extremely scarce in the cactus spine layers, where juniper needles were abundant. With both conifers easily available, it is difficult to see why piñon should be stored in quantity while juniper was preferred for daily feeding during the rest of the year. If the piñon layer were a food supply of *albigula* it was not the usual thing, for none of three other middens excavated at this locality contained such a layer. Indeed, not a single piñon needle was found in the cactus midden of den 490821-1. The five and one half inch layer of spines overlying the piñon needles in den 490821-2 seems much too deep to have been accumulated in a single year, because of the tremendous amount of cactus pulp that must be consumed to leave such a residue of spine areoles. Also, the top layer contained old spines and other buried material that looked more than a year old. In view of all these difficulties with the assumption of seasonal stratification, it seems to me more probable that each spine midden represented several years occupancy by *albigula* and that the intervening piñon midden represented a period of occupancy by *mexicana* or *cinerea.* Both the latter species eat many more piñon needles than does *abligula.* In the summer of 1949 the population of *albigula* there seemed to have been severely reduced, or wiped out, possibly by the unusually severe winter weather of the preceding January. Perhaps *mexicana,* which is able to live at higher elevations than *albigula,* fared better during the winter and produced young rats ready to move into the vacated dens of *albigula* in the summer of 1949. It would be of interest to determine the rates of accumulation of cactus spine middens by *albigula*, so that the histories of old dens such as this could be more reliably determined.

At Bondad an adult male Mexican wood rat (490615-5) and a subadult male white-throated wood rat (490615-4) were trapped on opposite sides of a single large sandstone block. When traps were set, it was thought that there might be two separate dens under the same block. Careful study of the midden under and around the boulder revealed no significant difference in composition or amount of food litter and den material on the two sides of the rock or through the connecting spaces between adjoining boulders. The two rats were caught on two sides of the same large continuous and nearly uniform midden. There was scarcely any cactus litter present, and the food litter contained mostly twigs and cuttings of skunkbush, sagebrush, and goldaster. The den materials present included some sage sticks, cow dung, horse dung, a few old dry joints of rat-tail cactus, a few stones, and a few sticks of cottonwood. All evidence indicated that there was a single large den established and occupied solely by *mexicana*. The *albigula* most likely wandered in from another den. Typical dens of *albigula* were present more than 25 yards away.

FOOD

The Mexican wood rat eats a wide variety of food plants, nearly all of which are shrubs or forbs. Some kinds are eaten in much larger quantities than others, but there seems to be no single kind or few kinds of plants providing the bulk of the food. Among the plants eaten most abundantly are scrub oak, skunkbush, mountain-mahogany, and juniper. But none of these preferred plants is at all essential to the existence of the Mexican wood rat. This species shares with the bushy-tailed wood rat the ability to subsist on whatever kinds of flowering plants may be easily available.

Concerning the parts of the plants eaten, foliage is consumed in much greater quantity than the fruits, flowers, stems, or woody parts of the plants. Conifer needles are important foods, more so than conifer seeds, but are less important than leaves of shrubs and forbs. Grasses and the succulent joints and fruits of cacti are only rarely eaten, and then only in small amounts.

The Mexican wood rat shows a marked dislike for cactus. This is all the more noticeable because of the general availability of cactus and its abundant use by other species of wood rats. When cactus debris is found at a den of this species it usually consists of only a few areoles or a single joint. At approximately half of the dens examined, the litter could be raked and spread with bare fingers without feeling any cactus spines.

The preferred food plants of *N. mexicana* are among the most abundant in the scrub oak belt and in the piñon—juniper belt. This is in keeping with the rather limited zonal range of this rat.

Although the plants available vary considerably according to the locality and habitat, the plants most utilized at any particular place usually are those most abundant and accessible. This results from unspecialized food requirements and the reluctance of the individual rat to go any farther from its den than necessary. The only indication of adaptive difference in food habits between subspecies is a possibly greater preference for *Yucca* by *scopulorum*, in comparison with *fallax*. *Yucca* is much more abundant in the range of *scopulorum*. But the number of dens studied at which *Yucca* was available was too small to ascertain if the preference for *Yucca* was statistically significant.

The food preferences of *N. mexicana* are more generalized than specialized, resembling most nearly those of *N. cinerea* and contrasting with the specialized habits of *N. albigula* and *N. micropus*. Lists of plants compiled from detailed examinations of 51 dens of Mexican wood rats indicate that nearly all the woody plants and forbs available to the rats are eaten, at least occasionally, to a slight extent. But there are significant differences in the amounts of each kind of plant eaten. Less than one fourth of all kinds of plants eaten are preferred foods.

In the present study the data obtained on food can best be presented separately for each subspecies of the Mexican wood rat, because of differences in the plants available in different parts of its range. Such treatment also facilitates comparison with sympatric species of wood rats.

N. mexicana fallax

Some preferred foods of *fallax* (from a study of only nine dens) are scrub oak, herbaceous *Artemisia*, skunkbush, mountain-mahogany, chokecherry, piñon, and juniper. Leaves and needles are eaten in quantity. Occasionally a few acorns, piñon seeds, and juniper berries are eaten.

Information concerning food is presented in the following paragraphs for each of the dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

One and One-half Miles Northwest of Golden, 6200 Feet

8 July 1948.—480708-1. ++ *Cercocarpus montanus*, - *Pinus ponderosa*, - *Juniperus scopulorum*; *Ribes cereum*, *Artemisia tridentata*, *Opuntia* sp. *Cercocarpus* twigs and dry leaves comprised approximately 90 percent of the food litter. The closest bush to the den was a squaw currant bush which had been scarcely pruned, if at all, and no debris of which had been recognized in the midden.

Seven Miles North and Four Miles West of Castle Rock, 6400 Feet

4 August 1948.—480804-1. * *Quercus gambellii,* * *Cercocarpus montanus,* * *Ribes cereum* or *inebrians,* * *Pinus ponderosa,* - *Onosmodium; Rubus deliciosus, Berberis repens.* Pine cones in the den probably furnished seeds for food. There were a few cut stalks of *Onosmodium* with leaves and nutlets.

480804-2. * *Quercus gambellii,* * *Symphoricarpos,* * *Rubus deliciosus,* - *Prunus virginiana,* - *Delphinium* sp., -- *Thermopsis; Juniperus scopulorum, Pinus ponderosa, Berberis repens.*

480804-4. * *Rubus deliciosus,* * *Quercus gambellii,* * *Prunus virginiana; Pinus ponderosa, Juniperus scopulorum, Berberis repens.*

480804-5. * *Berberis repens,* * *Quercus gambellii,* * *Cercocarpus montanus; Pinus ponderosa, Rubus deliciosus, Ribes cereum* or *inebrians.*

480804-6. + *Cercocarpus montanus,* * *Quercus gambellii,* * *Berberis repens,* - *Artemisia* (herbaceous sp.), - *Astragalus* sp., - *Pinus ponderosa,* -- *Rubus deliciosus,* -- *Thermopsis,* -- *Allium; Ribes cereum* or *inebrians, Fragaria.* Nearly all the bark had been gnawed off a small pine stick. Most of the litter was composed of mountain-mahogany twigs with the leaves bitten off. At all five of the dens studied at this locality there were twigs and leaf cuttings of scrub oak, but at only one of the dens were there any acorns or acorn shells.

Eighteen Miles South and Seven Miles West of Colorado Springs, 6200 Feet

16 September 1948.—480916-2. + *Rhus trilobata,* + *Melilotus,* * *Grindelia inornata angusta,* * *Conyza canadensis,* * *Tragopogon,* * *Prunus virginiana,* * *Artemisia ludoviciana ludoviciana,* * *Artemisia frigida,* * *Pinus edulis,* - *Juniperus monosperma,* - *Opuntia arborescens,* - *Lathyrus,* -- *Lesquerella; Symphoricarpos, Yucca glauca, Ribes* sp., *Eurotia lanata, Opuntia polyacantha, Opuntia humifusa, Gutierrezia, Chrysopsis foliosa, Lepidium alyssoides, Cirsium.* A chokecherry bush at the base of the rock sheltering the den had been pruned.

17 September 1948.—480917-1. + *Quercus gambellii,* + *Rhus trilobata,* + *Iva xanthifolia,* * *Pinus edulis,* * *Juniperus monosperma,* **Eurotia lanata,* * *Symphoricarpos* sp., * *Artemisia ludoviciana ludoviciana,* * *Melilotus,* * *Artemisia frigida,* - *Grindelia inornata angusta,* - *Opuntia humifusa,* - *Opuntia arborescens,* - *Lathyrus* sp., - *Ribes* sp., - *Chrysopsis foliosa,* - *Tragopogon* sp., -- *Gutierrezia,* -- *Onosmodium* sp., -- *Conyza canadensis,* -- *Gaura villosa,* -- *Mirabilis; Yucca glauca, Opuntia polycantha, Lepidium alyssoides.* The *Ribes* bush by the den had been pruned and seemed to be diseased or parasitized.

Two Miles East and One Mile South of Gold Hill, 7100 Feet

21 November 1949.—491121-1. * *Ribes cereum,* * *Juniperus scopulorum,* * *Helianthus rigidus,* * *Ceanothus fendleri,* - *Opuntia polyacantha,* -- *Yucca glauca,* -- *Artemisia ludoviciana; Pinus ponderosa, Pinus flexilis, Pseudotsuga taxifolia, Rubus delicosus, Jamesia americana, Prunus virginiana, Berberis repens, Artemisia frigida, Chrysopsis, Eriogonum, Geranium.* The sunflowers and *Ceanothus* in the vicinity of the den had been much pruned. Food debris of the cactus was a few spine areoles and dry fruits.

TABLE 16.—PLANTS AVAILABLE AND USED AS FOOD AT 9 DENS OF N. M. FALLAX (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Quercus gambellii	6	6	1
Artemisia (herbaceous spp.)	4	4	1
Rhus trilobata	2	2	2
Cercocarpus montanus	4	4	
Prunus virginiana	4	3 (75%)	
Pinus edulis	2	2	
Juniperus monosperma	2	2	
Melilotus	2	2	
Conyza canadensis	2	2	
Grindelia inornata angusta	2	2	
Tragopogon	2	2	
Opuntia arborescens	2	2	
Lathyrus	2	2	
Onosmodium	2	2	
Thermopsis	2	2	
Iva xanthifolia	1	1	1
Eurotia lanata	2	1 (50%)	1
Symphoricarpos	3	2 (67%)	
Artemisia frigida	3	2 (67%)	
Rubus deliciosus	6	3 (50%)	
Juniperus scopulorum	4	2 (50%)	
Pinus ponderosa	7	3 (43%)	
Ribes cereum	5	2 (40%)	
Opuntia (*Platyopuntia*)	6	2 (33%)	
Berberis repens	6	2 (33%)	
Ribes (*Grossularia*)	2	1 (50%)	
Gutierrezia	2	1 (50%)	
Yucca glauca	3	1 (33%)	
Chrysopsis	3	1 (33%)	
Lepidium alyssoides	2		
(single occurrences grouped irrespective of preference)			
Ceanothus fendleri	1	1	
Helianthus rigidus	1	1	
Astragalus	1	1	
Delphinium	1	1	
Gaura villosa	1	1	
Mirabilis	1	1	
Lesquerella	1	1	
Allium	1	1	
Pinus flexilis	1		
Pseudotsuga taxifolia	1		
Geranium	1		
Fragaria	1		
Artemisia tridentata	1		
Eriogonum	1		
Jamesia americana	1		

A summary of food data obtained at all nine dens of *N. m. fallax* is presented in Table 16 in order to show the relative preference for each kind of food plant. High relative preference is indicated by high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants to the dens were also considered in arranging the plants roughly in order of decreasing preference.

N. mexicana scopulorum

Some preferred foods of *scopulorum* (from a study of only five dens) are the foliage of mugwort, *Yucca glauca,* skunkbush, and *Brickellia.* Fruit capsules of the *Yucca* were also gnawed. Flower cuttings of mugwort and an unidentified shrubby *Artemisia* were gathered in lesser amount than the foliage cuttings.

Information concerning food is presented in the following paragraphs for each of the dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Two Buttes Reservoir, 4200 Feet

9 May 1950.—500509-1. * *Yucca glauca,* * *Brickellia,* * *Panicum virgatum,* * *Artemisia ludoviciana mexicana,* - *Xanthium,* -- *Helianthus; Artemisia filifolia, Rhus trilobata, Opuntia humifusa, Buchloe dactyloides.* The food litter of *Yucca* consisted of leaf blades and fruit pods.

10 May 1950.—500510-1. + *Brickellia,* * *Yucca glauca,* * *Artemisia ludoviciana mexicana,* - *Gutierrezia,* -- *Opuntia humifusa; Artemisia filifolia, Rhus trilobata, Vitis, Buchloe dactyloides, Cirsium.*

Two Buttes Peak, 4600 and 4650 Feet

9 May 1950.—500509-9. + *Rhus trilobata,* * *Artemisia* (shrub sp.), * *Artemisia ludoviciana,* * *Yucca glauca,* - *Sporobolus cryptandrus,* -- *Cirsium; Atriplex canescens, Bouteloua gracilis.* The den was screened by a dense thicket of skunkbush, the branches of which had been pruned and the bark of which had been gnawed. The thicket was in flower but not yet in leaf. A storage supply of mixed food cuttings contained skunkbush twigs and cuttings estimated at 50 percent of the total, which was at least three gallons.

500509-10. + *Rhus trilobata,* * *Yucca glauca,* * *Sporobolus cryptandrus,* - *Artemisia* (shrub sp.), - *Artemisia ludoviciana,* - *Atriplex canescens,* - *Salsola kali; Opuntia humifusa, Bouteloua gracilis.* Most of the food litter looked to be old.

Three Miles Northwest of Higbee, 4300 Feet

16 May 1950.—500516-2. * *Brickellia californica,* * *Artemisia ludoviciana,* * *Rhus trilobata,* * *Cirsium,* * *Salsola kali,* * *Opuntia arborescens,* * *Opuntia humifusa,* * *Verbena* sp., * *Ratibida tagetes,* * *Solanum elaeagnifolium,* * *Astragalus* cf. *A. pectinatus,* - *Senecio spartioides,* - *Asclepias,* -- *Juniperus monosperma,* -- *Yucca glauca; Gutierrezia, Atriplex canescens, Opuntia polyacantha, Bouteloua gracilis, Helianthus.* The juniper cuttings may have come from two seedlings growing on the slope below, both of which had been pruned.

A summary of data on food obtained at five dens of *N. m. scopulorum* is presented in Table 17 in order to show the relative preference for each kind of plant. The data are unfortunately too few to allow significant comparisons with other subspecies.

TABLE 17.—PLANTS AVAILABLE AND USED AS FOOD AT 5 DENS OF N. M. SCOPULORUM (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Artemisia ludoviciana	5	5	1
Yucca glauca	5	5	1
Brickellia	3	3	1
Rhus trilobata	5	3	2
Artemisia sp. (shrub)	2	2	1
Solanum elaeagnifolium	1	1	1
Verbena	1	1	1
Salsola kali	2	2	....
Sporobolus cryptandrus	2	2	....
Astragalus cf. *A. pectinatus*	1	1	....
Senecio spartioides	1	1	....
Juniperus monosperma	1	1	....
Opuntia arborescens	1	1	....
Panicum virgatum	1	1	....
Asclepias	1	1	....
Ratibida tagetes	1	1	....
Xanthium	1	1	....
Cirsium	3	2	....
Gutierrezia sarothrae	2	1	....
Helianthus	2	1	....
Opuntia (*Platyopuntia*)	5	2	....
Atriplex canescens	3	1	....
Vitis	1	....	....
Artemisia filifolia	2	....	....
Buchloe dactyloides	2	....	....
Bouteloua gracilis	3	....	....

N. mexicana inopinata

Among the most preferred food plants of *inopinata* are scrub oak, mountain-mahogany, junipers, herbaceous *Artemisia,* saltbush, chokecherry, rabbitbrush, serviceberry, piñon, ponderosa pine, and skunkbush. The leaves and needles of these plants are eaten in considerable amounts. Acorns, juniper berries, and piñon seeds are less frequently eaten and nearly always much exceeded in bulk by the amounts of foliage eaten. The pulpy husks are eaten from the juniper fruits, but the nutlets seem generally to be discarded. Those nutlets that have been cracked open for the seeds are probably debris left by squirrels or chipmunks. Seed plumes of mountain-mahogany are sometimes scattered among the food litter, but these are seemingly dropped there by the wind. Whether the rats eat the seeds is not known. Flower cuttings of *Artemisia* are frequently gathered, as well as the foliage cuttings.

Even when easily accessible close to a den the following plants seem to be but little used as food by *N. m. inopinata:* cottonwood, snakeweed, paloblanco, cacti, rose, willow, and mountain sage.

Information concerning food is presented in the following paragraphs for each of 37 dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Bondad, 6050 Feet

15 June 1949.—490615-1. * *Cercocarpus montanus,* * *Juniperus scopulorum,* -- *Artemisia tridentata; Quercus gambellii, Rhus trilobata, Prunus virginiana, Fendlera rupicola, Opuntia polyacantha?.* A joint had been bitten off the cactus growing in front of the entrance to the den, but no areoles were found in the food litter.

490615-2. * *Quercus gambellii,* * *Rhus trilobata,* - *Opuntia polyacantha?; Juniperus scopulorum, Artemisia tridentata, Fendlera rupicola, Berberis repens, Melilotus.* Scrub oak and skunkbush had been pruned. Many stalks of sweet clover had been snipped off the plants 30 feet from the den, but none was found in the food litter.

490615-5. + *Rhus trilobata,* + *Artemisia tridentata,* + *Chrysopsis villosa,* + *Artemisia ludoviciana,* * *Chrysothamnus,* - *Prunus virginiana,* - *Amelanchier,* - *Opuntia rhodantha,* - *Opuntia davisii,* - *Chenopodium; Juniperus scopulorum, Pinus edulis, Ribes aureum, Forestiera neomexicana, Clematis ligusticifolia, Mammillaria vivipara, Sphaeralcea* cf. *S. parvifolia, Sphaeralcea coccinea elata.* Although no cuttings of *Ribes* were found at the den, a bush had been pruned.

490615-8. * *Rhus trilobata,* * *Ribes aureum,* * *Juniperus scopulorum,* * *Prunus virginiana,* * *Amelanchier* sp., * *Chrysothamnus* sp., * *Gutierrezia,* * *Clematis ligusticifolia,* * *Sphaeralcea* cf. *S. parvifolia,* - *Hymenoxys acaulis ivesiana,* - *Opuntia rhodantha,* - *Artemisia tridentata,* -- *Fendlera rupicola; Salix, Populus angustifolia, Forestiera neomexicana, Berberis repens, Yucca baccata, Opuntia davisii, Chrysopsis villosa, Artemisia ludoviciana. Prunus* and *Ribes* were pruned.

490615-10. + *Juniperus scopulorum,* + *Artemisia tridentata,* * *Opuntia rhodantha,* * *Forestiera neomexicana,* * *Rhus trilobata,* * *Chrysothamnus* sp.; *Populus angustifolia, Salix, Berberis repens, Opuntia davisii, Clematis ligusticifolia.* The food debris of paloblanco was twigs from which the leaves had been eaten off. Bushes of paloblanco had been pruned.

One Mile Southwest of Gateway, 4600 Feet

19 June 1949.—490619-4. + *Juniperus utahensis,* - *Lepidium montanum,* - *Hymnopappus lugens?,* - *Penstemon* sp., -- *Stanleya pinnata pinnata; Pinus edulis, Artemisia tridentata, Coleogyne ramosissima, Rhus trilobata, Opuntia polyacantha.*

490619-5. ++ *Cowania mexicana; Juniperus utahensis, Pinus edulis, Artemisia tridentata, Coleogyne ramosissima.* Food litter was scarce, almost entirely cuttings, flowers and seed plumes of *Cowania.*

490619-9. * *Juniperus utahensis,* * *Coleogyne ramosissima,* * *Penstemon* sp., * *Lepidium montanum,* * *Sphaeralcea parvifolia; Pinus edulis, Artemisia tridentata, Rhus trilobata, Yucca angustissima, Opuntia phaeacantha.*

490619-10. + *Juniperus utahensis,* + *Fraxinus anomala,* + *Atriplex canescens,* * *Coleogyne ramosissima,* * *Lepidium montanum,* -- *Ephedra torreyana; Pinus edulis, Artemisia tridentata, Opuntia polyacantha. Ephedra* was pruned.

Two and One-half Miles South and One Mile West of Gateway, 5500 Feet

21 June 1949.—490621-3. * *Amelanchier utahensis,* * *Brickellia californica,* - *Salsola kali,* -- *Juniperus utahensis,* -- *Rosa* sp.; *Pinus edulis, Populus acuminata, Artemisia tridentata, Ephedra viridis, Philadelphus microphyllus, Lepidium montanum, Sphaeralcea parvifolia.*

One Mile East of Naturita, 5900 Feet

26 June 1949.—490626-4. + *Pinus edulis,* * *Juniperus utahensis,* * *Amelanchier* sp., * *Artemisia tridentata; Chrysothamnus nauseosus, Rhus trilobata, Opuntia polyacantha, Chrysopsis.* The food litter was mostly piñon foliage cuttings with a few empty piñon shells. There were no cactus spines in the midden.

490626-8. + *Pinus edulis,* * *Juniperus utahensis,* * *Amelanchier,* - *Atriplex canescens,* - *Opuntia polyacantha; Ephedra viridis, Rhus trilobata, Chrysothamnus nauseosus, Chrysopsis.* A clump of serviceberry had been heavily pruned.

490626-10. + *Pinus edulis,* + *Juniperus utahensis,* * *Amelanchier* sp., * *Atriplex canescens,* * *Chrysothamnus nauseosus; Rhus trilobata, Artemisia tridentata.*

One Mile North of Cahone, 6900 Feet

2 August 1949.—490802-4. + *Juniperus utahensis,* + *Pinus edulis,* * *Chrysothamnus nauseosus,* * *Peraphyllum ramosissimum,* * *Purshia tridentata,* - *Chrysopsis,* - *Gutierrezia,* -- *Opuntia polyacantha; Artemisia tridentata, Rhus trilobata.* Old cuttings of juniper and piñon comprised most of the litter. The remains of goldaster and snakeweed were flower cuttings. A bush of squaw-apple near the den had been pruned.

Three Miles West and Two Miles South
of Cahone, 7000 Feet

5 August 1949. — 490805-2. + *Juniperus utahensis,* + *Pinus edulis,* * *Amelanchier utahensis* and/or *Cercocarpus montanus; Purshia tridentata, Gutierrezia, Echinocereus coccineus, Penstemon bridgesii.* Some twigs without leaves came from either *Amelanchier* or *Cercocarpus,* but none of these could be distinguished with certainty.

Four Miles West and Two Miles South
of Cahone, 7000 Feet

1 August 1941. — 490801-5. + *Juniperus utahensis,* + *Cercocarpus montanus,* - *Pinus edulis; Ephedra viridis, Amelanchier utahensis, Rhus trilobata, Gutierrezia, Penstemon bridgesii.*

20 August 1949.—490820-1. + *Juniperus utahensis,* + *Cercocarpus montanus,* - *Pinus edulis,* - *Ephedra viridis,* -- *Lepidium montanum; Amelanchier utahensis, Echinocereus coccineus, Gutierrezia, Penstemon bridgesii.* Several fruits had been gnawed off the two clumps of pincushion cactus that grew in front of the den, but by thoroughly searching and sifting the midden with my bare hands I was able to find only three spine areoles, and they did not seem to have been gnawed.

Six and One-half Miles East and Two Miles South of Cahone, 6800 Feet

19 August 1949.—490819-1. + *Cercocarpus montanus,* * *Juniperus utahensis,* * *Pinus edulis,* * *Chrysothamnus nauseosus,* * *Opuntia fragilis,* * *Opuntia phaeacantha,* * *Yucca baccata,* * *Amelanchier,* -- *Quercus gambellii,* -- *Rosa* sp., -- *Echinocereus coccineus; Rhus trilobata, Gutierrezia sarothrae.* The nearest available *Opuntia fragilis* grew 50 yards downslope from the den. A more abundant supply grew 150 yards from the den. Two acorn shells were in the food litter, but no scrub oaks were seen within 100 feet of the den. Many leaf blades of *Yucca baccata* had been gnawed or cut into sections.

Eight Miles North and Three Miles East of Egnar, 5800 Feet

21 August 1949.—490821-1. * *Chenopodium* sp., * *Gutierrezia,* -- *Artemisia tridentata; Juniperus utahensis, Pinus edulis, Atriplex confertifolia, Forestiera neomexicana, Ephedra torreyana?, Opuntia hystricina, Echinocactus whipplei, Echinocereus coccineus, Salsola kali.* The food remains of sagebrush was one leaf cutting. In addition to the food litter reported above, all of which was green and recently gathered, there was a bed of old dry brown *Opuntia hystricina* spines and juniper needles with a few old *Salsola* cuttings. The composition and age of the older material indicates that it was accumulated by *Neotoma albigula,* not by *N. mexicana,* the more recent occupant of the den.

490821-2. - *Juniperus utahensis,* -- *Chenopodium* sp., -- *Chrysothamnus* sp.; *Pinus edulis, Artemisia tridentata, Atriplex confertifolia, Opuntia hystricina, Gutierrezia, Salsola kali.* Food litter reported above is all that can safely be attributed to the most recent occupant of the den. But this scanty material rested on a deep old midden of *Opuntia hystricina* spines mixed with many juniper needles, a few *Atriplex* twigs, a few piñon needles and a few spines of *Echinocactus whipplei.* The old midden undoubtedly was built up by *Neotoma albigula,* not *N. mexicana.* A buried, two and one-half inch layer of piñon needles interbedded between layers of cactus spines probably represents an earlier period of occupancy by *N. mexicana* or *cinerea* preceded and followed by periods of occupancy by *N. albigula.* For further discussion of the dens at this locality and the relationship of these two species see pages 421 to 423.

Eighteen Miles North and One Mile East of Farmington, 6000 Feet, New Mexico

10 August 1949.—490810-1. + *Atriplex canescens,* * *Juniperus utahensis,* * *Artemisia tridentata,* - *Chrysothamnus nauseosus,* -- *Rhus trilobata; Pinus edulis, Juniperus monosperma, Sarcobatus vermiculatus, Quercus gambellii, Yucca baccata, Salsola kali, Chrysopsis.* Saltbush, juniper, and rabbitbrush were pruned.

490810-4. + *Ribes* cf. *R. inerme*, + *Rhus trilobata*, + *Atriplex canescens*, * *Juniperus utahensis*, * *Ephedra viridis*, * *Artemisia ludoviciana*, -- *Quercus gambellii; Pinus edulis, Artemisia tridentata, Forestiera neomexicana, Yucca baccata, Chrysothamnus nauseosus, C. greenei, Opuntia polyacantha, Clematis ligusticifolia, Chrysopsis.*

490810-5. + *Cercocarpus montanus*, + *Amelanchier utahensis*, + *Pinus edulis*, * *Juniperus utahensis*, * *Brickellia scabra*, * *Chenopodium incanum*, * *Gutierrezia* sp.; *Rhus trilobata, Artemisia tridentata, Ephedra viridis, Opuntia polyacantha.* Food litter of *Cercocarpus* was a mixture of twigs and seed plumes. There were a quart of piñon cuttings with scarcely any needles bitten off, and a green piñon cone from which the nuts had been gnawed out.

One Mile Southeast of Durango, 5700 Feet

24 August 1949.—490824-1. + *Berberis repens*, * *Quercus gambellii*, * *Chrysopsis*, * *Symphoricarpos* sp., - *Prunus virginiana*, -- *Salsola kali*, -- *Smilacina racemosa*, -- *Artemisia ludoviciana; Pinus edulis, Juniperus utahensis, Artemisia tridentata, Rhus trilobata, Clematis* sp.

490824-2. + *Chrysothamnus nauseosus*, * *Quercus gambellii*, * *Symphoricarpos* sp., * *Berberis repens*, - *Artemisia tridentata*, -- *Marrubium vulgare; Pinus edulis, Juniperus utahensis, Peraphyllum ramosissimum, Rhus trilobata, Artemisia frigida, Opuntia davisii, Salsola kali.*

Three Miles West and One Mile South of Durango, 7200 Feet

31 August 1949.—490831-1. + *Quercus gambellii*, + *Rhus trilobata*, * *Purshia tridentata*, * *Berberis repens*, * *Juniperus scopulorum*, * *Symphoricarpos*, * *Cercocarpos montanus*, * *Amelanchier alnifolia*, *? *Peraphyllum ramosissimum*, * *Pinus ponderosa*, * *Pinus edulis*, - *Pseudotsuga taxifolia*, - *Opuntia*, -- *Berberis fendleri*, -- *Brickellia californica*, -- *Penstemon* sp.; *Rhus radicans, Gutierrezia, Rosa* sp., *Eriogonum jamesii. Peraphyllum* had been pruned, but its twigs among the food litter could not be distinguished with certainty from those of *Amelanchier.*

490831-2. + *Quercus gambellii*, * *Peraphyllum ramosissimum*, * *Symphoricarpos* sp., * *Amelanchier alnifolia*, * *Chrysothamnus nauseosus*, * *Juniperus scopulorum*, * *Pinus ponderosa*, * *Pinus edulis*, * *Pseudotsuga taxifolia*, * *Berberis repens*, * *Rhus trilobata*, * *Purshia tridentata*, * *Penstemon* sp., - *Artemisia ludoviciana*, - *Aster arenosus*, - *Bouteloua gracilis*, -- *Eriogonum jamesii*, -- *Yucca baccata*, -- *Lathyrus* sp.; *Rosa, Rhus radicans.* More than a bushel of dry green oak cuttings were crammed in a rock cleft. An old storage supply of mixed, brown cuttings, containing much *Peraphyllum*, filled a lower crevice.

Two Miles East of Durango, 7500 Feet

10 September 1949.—490910-1. + *Juniperus utahensis*, * *Quercus gambellii*, * *Chrysopsis*, * *Yucca baccata*, * *Cercocarpus montanus*, * *Eurotia lanata*, * *Amelanchier*, * *Penstemon* sp., - *Physalis* sp., - *Pinus ponderosa*, - *Opuntia polyacantha* or *rhodantha?; Pinus edulis, Rhus trilobata, Eriogonum jamesii, Gutierrezia, Berberis repens.* The bark had been eaten off a twig of ponderosa pine. A fruit of prickly pear had been half eaten and was not identifiable to one or other of the two species of *Opuntia* present.

Six Miles East and Seventeen Miles South of Cortez, 5600 Feet

15 September 1949.—490915-2. + *Juniperus utahensis,* + *Cercocarpus montanus,* + *Sarcobatus vermiculatus,* - *Chrysothamnus nauseosus,* - *Opuntia polyacantha,* - *Atriplex confertifolia; Pinus edulis, Artemisia tridentata, Ephedra viridis, Amelanchier, Purshia tridentata, Gutierrezia.*

Five Miles East and Twelve Miles South of Mancos, 7000 Feet

11 October 1949.—491011-1. + *Juniperus utahensis,* * *Cercocarpos montanus,* * *Artemisia dracunculus glauca?,* * *Pinus edulis,* * *Eriogonum simpsoni,* * *Lepidium montanum,* - *Opuntia polyacantha; Artemisia tridentata, Amelanchier, Gutierrezia, Opuntia davisii.* The food remains of cactus were a few partly eaten fruits.

Five Miles East of Cortez, 6400 Feet

16 October 1949.—491016-1. + *Opuntia polyacantha,* + *Pinus edulis,* * *Juniperus utahensis; Amelanchier utahensis, Artemisia tridentata, Gutierrezia, Chenopodium, Salsola kali, Rumex crispus.* The midden contained a large quantity of cactus spines, but mixed with such an amount of juniper needles that the spines did not hold together in a compact mass. The amount of cactus spines was much more than was commonly found at dens of *N. mexicana,* but less than the amount nearly always present at dens of *N. albigula.* Possibly this midden was accumulated, at least in part, by *N. albigula.*

Two Miles Northeast of Bondad, 6100 Feet

24 October 1949.—491024-4. + *Rhus trilobata,* + *Alnus tenuifolia,* + *Artemisia ludoviciana,* * *Quercus gambellii,* * *Gaura coccinea,* * *Mirabilis oxybaphoides,* * *Clematis ligusticifolia,* * *Prunus virginiana,* * *Juniperus scopulorum,* * *Verbascum thapsus,* * *Bromus,* * *Muhlenbergia racemosa,* - *Melilotus,* - *Juniperus utahensis,* - *Chrysothamnus nauseosus,* - *Marrubium vulgare,* - *Agrostis,* -- *Pinus edulis,* -- *Chrysopsis,* -- *Conyza canadensis,* -- *Sphaeralcea coccinea elata; Salix, Purshia tridentata, Artemisia tridentata, Amelanchier utahensis, Rosa, Opuntia phaeacantha, Opuntia polyacantha, Opuntia davisii, Gutierrezia, Salsola kali, Cirsium.* Much dry grass *(Bromus, Muhlenbergia,* and *Agrostis)* that appeared to be partly eaten was on the top and sides of the house. Most other food material was crammed into spaces and passages within the house.

491024-6. + *Opuntia davisii,* * *Quercus gambellii,* * *Opuntia phaeacantha,* * *Opuntia rhodantha,* * *Sphaeralcea* cf. *S. parvifolia,* * *Berberis fendleri,* -- *Populus wislizeni,* -- *Cirsium* sp.; *Populus angustifolia, Pinus edulis, Juniperus utahensis, Rhus trilobata, Artemisia tridentata, Prunus virginiana, Chrysothamnus nauseosus, Gutierrezia, Verbascum thapsus.* Small amounts of rat-tail cactus and acorns in the den were probably stored food. Food litter of scrub oak consisted of partly eaten leaves and acorn shells.

491024-7. + *Artemisia ludoviciana,* + *Quercus gambellii,* * *Sphaeralcea* cf. *S. parvifolia,* * *Rhus trilobata,* * *Prunus virginiana,* * *Chrysopsis,* * *Salsola kali,* * *Opuntia davisii,* - *Bromus,* -- *Chrysothamnus nauseosus,* -- *Gutierrezia,* -- *Marrubium vulgare,* -- *Chenopodium* sp.; *Populus wislizeni, Populus angustifolia, Pinus edulis, Juniperus utahensis, Amelanchier utahensis, Artemisia tridentata, Artemisia frigida, Berberis fendleri, Verbascum thapsus.* Globe mallow growing in the vicinity of the den had been pruned.

TABLE 18.—PLANTS AVAILABLE AND USED AS FOOD AT 37 DENS OF N. M. INOPINATA (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE).

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Quercus gambellii	14	12 (86%)	5
Cercocarpus montanus	10	10 (100%)	1
Juniperus utahensis	29	23 (79%)	2
Juniperus scopulorum	9	7 (78%)	2
Atriplex canescens	6	6 (100%)	1
Artemisia (herbaceous spp.)	9	7 (78%)	2
Prunus virginiana	8	6 (75%)	2
Chrysothamnus	19	13 (68%)	...
Amelanchier	19	12 (63%)	1
Pinus edulis	31	16 (52%)	2
Pinus ponderosa	4	4 (100%)	1
Rhus trilobata	25	11 (44%)	2
Symphoricarpos	4	4 (100%)	...
Peraphyllum ramosissimum	4	3 (75%)	1
Marrubium vulgare	3	3 (100%)	...
Chenopodium	6	5 (83%)	...
Lepidium montanum	6	5 (83%)	...
Brickellia	3	3 (100%)	...
Sphaeralcea	8	5 (62%)	1
Chrysopsis	13	6 (46%)	1
Opuntia davisii	8	3 (38%)	1
Opuntia rhodantha	7	5 (71%)	...
Penstemon	8	5 (62%)	...
Mirabilis oxybaphoides	2	2 (100%)	1
Berberis fendleri	4	3 (75%)	...
Berberis repens	9	5 (56%)	...
Purshia tridentata	6	3 (50%)	...
Yucca baccata	6	3 (50%)	...
Pseudotsuga taxifolia	2	2 (100%)	...
Stanleya	2	2 (100%)	...
Ribes (*Grossularia*)	3	2 (67%)	...
Yucca (dry-fruited spp.)	3	2 (67%)	...
Artemisia tridentata	28	10 (36%)	1
Clematis	6	2 (33%)	1
Salsola kali	11	5 (45%)	...
Ephedra	10	4 (40%)	...
Aster	2	2 (100%)	...
Bromus	2	2 (100%)	...
Atriplex confertifolia	4	2 (50%)	...
Coleogyne ramosissima	4	2 (50%)	...
Eriogonum	4	2 (50%)	...
Opuntia phaeacantha	4	2 (50%)	...
Opuntia polyacantha	13	5 (38%)	...
Rosa	6	2 (33%)	...
Gutierrezia	19	4 (21%)	...
Sarcobatus vermiculatus	2	1 (50%)	...
Cirsium	2	1 (50%)	...
Melilotus	3	1 (33%)	...
Fendlera rupicola	3	1 (33%)	...
Verbascum thapsus	3	1 (33%)	...

TABLE 18.—*Concluded*

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Forestiera neomexicana	5	1 (20%)	
Echinocereus coccineus	5	1 (20%)	
Populus	7	1 (14%)	
Rhus rydbergii	2		
Opuntia hystricina	2		
Artemisia frigida	3		
Salix	3		
(single occurrences grouped irrespective of preference)			
Alnus tenuifolia	1	1	1
Gaura coccinea	1	1	1
Opuntia fragilis	0	1	
Cowania mexicana	1	1	
Fraxinus anomala	1	1	
Eurotia lanata	1	1	
Hymenoxys acaulis	1	1	
Smilacina racemosa	1	1	
Lathyrus	1	1	
Hymenopappus lugens?	1	1	
Achillea lanulosa	1	1	
Conyza canadensis	1	1	
Physalis	1	1	
Muhlenbergia racemosa	1	1	
Agrostis	1	1	
Bouteloua gracilis	1	1	
Juniperus monosperma	1		
Philadelphus microphyllus	1		
Rumex crispus	1		
Tetradymia spinosa	1		
Echinocactus whipplei	1		
Echinocactus simpsonii	1		

Seven and One-half Miles West of Montrose, 6000 Feet

2 November 1949.—491102-3. + *Atriplex canescens,* * *Juniperus utahensis,* * *Artemisia tridentata,* * *Yucca* sp., - *Opuntia polyacantha,* - *Salsola kali,* -- *Mirabilis multiflora; Populus wislizeni, Opuntia rhodantha, Echinocactus simpsonii, Gutierrezia.* About two gallons of cuttings, mostly *Atriplex,* were stuffed into vertical clefts in sandstone rimrock.

Two and One-half Miles South of Fruita, 4600 Feet

6 November 1949.—491106-4. + *Juniperus utahensis,* + *Opuntia rhodantha,* * *Atriplex confertifolia,* * *Yucca angustissima?,* * *Salsola kali,* * *Stanleya albescens,* - *Ephedra viridis,* - *Artemisia tridentata,* - *Pinus edulis; Chrysothamnus greenei, Chrysopsis, Tetradymia spinosa, Echinocereus coccineus, Gutierrezia.* Areoles of cactus were abundant in the midden, but not enough for the spines to be enmeshed in a compact spiny mass.

Two Miles West and One Mile South of Chromo, 7200 Feet

16 November 1949.—491116-3. + *Quercus gambellii,* * *Juniperus scopulorum,* * *Pinus ponderosa,* * *Berberis repens,* - *Rhus trilobata,* -- *Prunus virginiana,* -- *Achillea lanulosa,* -- *Berberis fendleri,* -- *Aster; Rosa, Artemisia frigida, Chrysopsis, Artemisia ludoviciana, Melilotus.* At least five bushels of scrub oak cuttings had been crammed into a large diagonal cleft through the sandstone boulder sheltering the den.

A summary of food data obtained at all 37 dens of *N. m. inopinata* is presented in Table 18 in order to show the relative preference for each kind of plant. The quantities of each plant in the food litter and the proximities of the available plants to the dens were also considered in arranging the plants roughly in order of decreasing preference.

Three wood rats were trapped at dens seven and one-half miles west of Montrose on 2 November 1949. Only one den was examined in detail (see page 435, den 491102-3). At den 491102-2 there were two old stalks of *Marrubium vulgare* but almost no other food litter. Clumps of *Marrubium* growing in front of the den had been pruned a little. Another den in the same rimrock, at which no rat was caught, contained more than two quarts of cuttings of *Atriplex canescens* and *Artemisia tridentata.* Most of the latter bore flower stalks. There were also some cuttings of *Salsola kali* and *Marrubium vulgare.*

STORAGE

The storage habit is strongly developed in the Mexican wood rat. Although food stores in considerable amount may be present at any season of the year, the greatest collecting activity seems to take place in late summer and fall. Quantities of food gathered at that season greatly exceed the amounts that may be brought in during spring or early summer. Stored food consists almost entirely of dried foliage cuttings. The green color and well preserved condition of the fresh stores after having been crammed into the storage spaces suggest that they may first have been "cured" by spreading out in the open air until dry before being packed away.

Many food stores could have been present but not discovered during the examinations of the dens, since the inner recesses of dens of this wood rat were nearly always deep in inaccessible rock shelters. Possibly stores of fruits, such as piñon nuts, juniper berries, acorns, or seeds may have been so hidden, but no evidence of such fruits was found except as a small part of larger accessible stores of leaf cuttings.

The large amounts of food stored in the fall are in contrast to the small and relatively useless amounts of sticks and other den material gathered. The latter are seldom sufficient to add to the

FIG. 1. Rock outcrop sheltering dens of the Mexican wood rat in the Scrub oak—scattered pines community, 3 miles west and 1 mile south of Durango, 7200 feet elevation.

FIG. 2. The Juniper—sagebrush habitat of *N. mexicana* and *N. cinerea* by the Colorado-New Mexico line north of Farmington.

PLATE 24

FIG. 1. View southwest from Daniels Park showing scrub oak chaparral on steep slopes and scattered ponderosa pines on the rim of the upland. *N. mexicana fallax* inhabits rock outcrops along the rim.

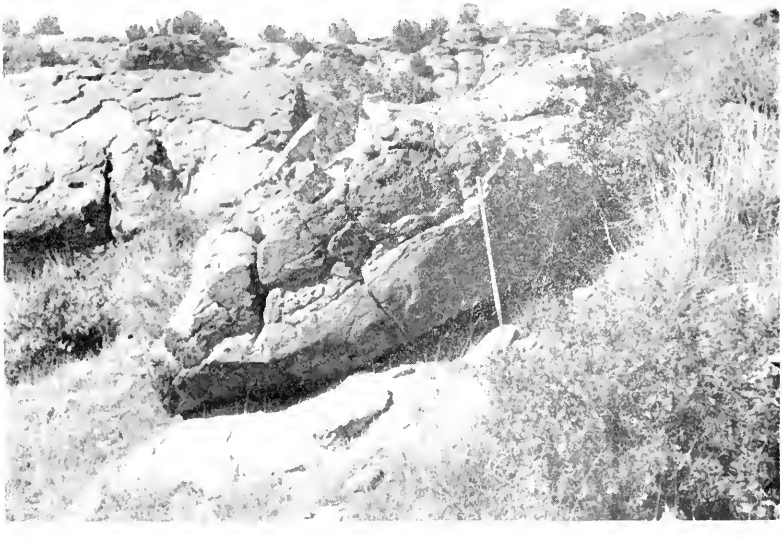


FIG. 2. Junipers on the rim of the High Plains bordering the valley of Gallinas Creek at Regnier. Broken blocks of Dakota sandstone lying on the slope provide good shelter for *N. mexicana* and *N. albigula*.

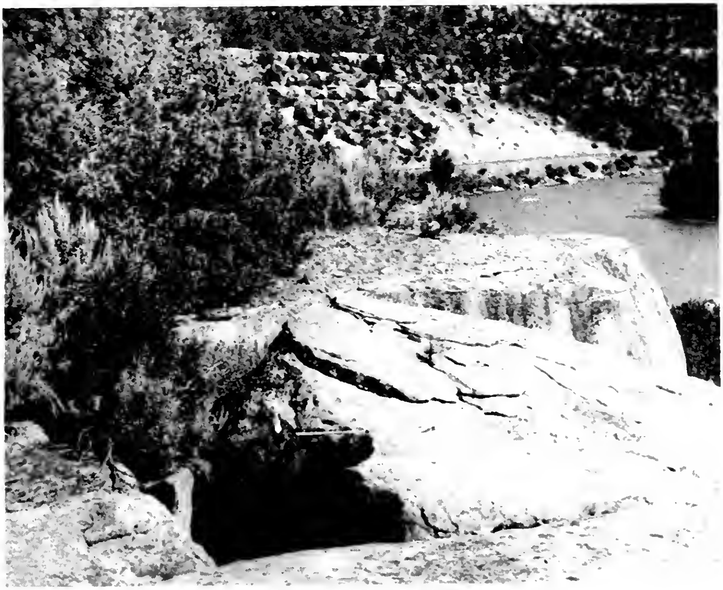


Fig. 1. Sandstone rim on the north side of the Animas Valley at Bondad, the type locality of *N. a. laplataensis*. The outcrop and fallen blocks provide shelter for both *N. albigula* and *N. mexicana*.

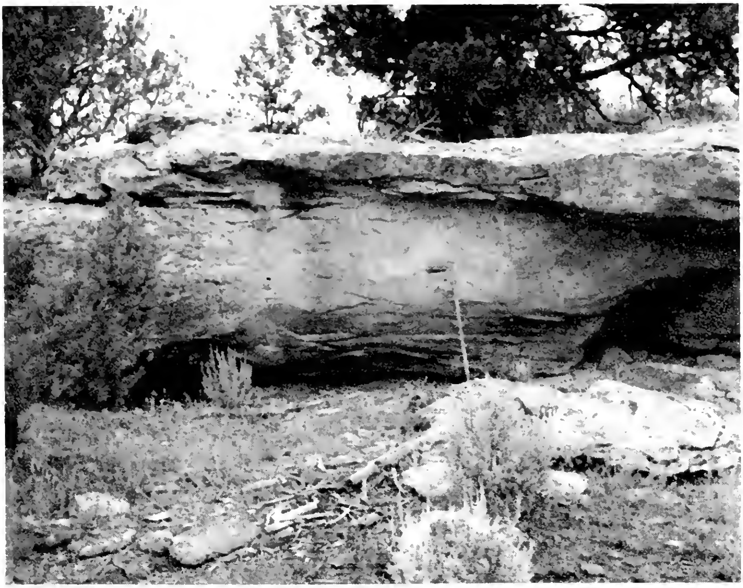


Fig. 2. Rim outcrop of sandstone sheltering a den of *N. mexicana* in the Piñon—juniper association one mile north of Cahone.

FIG. 1. Den of the Mexican wood rat (491016-1) in crevices of sandstone outcrop five miles east of Cortez.

FIG. 2. Den of the Mexican wood rat (500509-1) at base of cliff in valley below Two Buttes Reservoir. The midden on the floor of the cave lies on a bedding plane of red sandstone.

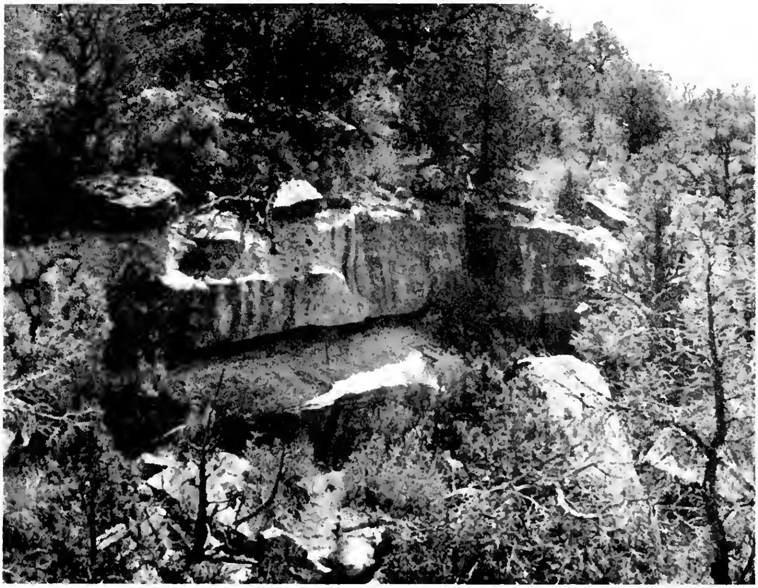


FIG. 1. Sandstone overhang and long sloping block 6½ miles east and 2 miles south of Cahone. The block shields a den of *N. mexicana*, shown in Fig. 2.

FIG. 2. Den of *N. mexicana* (490819-1) containing an unusually large mass of sticks behind the fallen block of sandstone shown in Fig. 1.

PLATE 28

FIG. 1. House of *N. mexicana* (491024-4) composed mostly of twigs and other food litter in thicket of skunkbush two miles northeast of Bondad. Part of the thicket was chopped away to expose the den.

FIG. 2. Twigs and sticks, seeming to serve no useful purpose, piled on rock at base of cliff by *N. mexicana* two miles northeast of Bondad.

FIG. 3. Dried leaf cuttings of scrub oak stored in spaces between rocks at base of cliff by *N. mexicana* two miles northeast of Bondad.

protection already provided by the rocks which this wood rat nearly always chooses for its den. The few "houses" found had been constructed almost entirely of twigs, stems, shoots, and other food litter, frequently intermixed with uneaten food cuttings. The collecting instinct of the Mexican wood rat seems well adapted to its living conditions. The moderately cold and long winters are well provided for by the large amounts of food laid up, but little effort is wasted adding building material to the already adequate den shelters.

Two dens studied of *N. mexicana fallax* contained stored food. At den 480916-2, the principal vertical crevice through the sheltering boulder contained more than a gallon of dry green cuttings of *Rhus trilobata.* At den 480917-1 the space under and between two abutting sandstone blocks was crammed with approximately two gallons of cuttings of *Rhus trilobata, Quercus gambellii, Iva xanthifolia, Eurotia lanata,* and *Artemisia ludoviciana.*

Two dens of *N. mexicana scopulorum* contained stored food. There were at least three gallons of mixed plant cuttings at den 500509-9 under a pile of boulders. The storage consisted of roughly 50 per cent *Rhus trilobata,* 25 per cent *Yucca glauca,* and 25 per cent *Artemisia* (two species). There was more than a bushel of mixed cuttings stored at den 500516-2. The kinds of plants included were *Rhus trilobata, Brickellia californica, Artemisia ludoviciana, Verbena* sp., and *Solanum eleagnifolium.*

Eight dens of *N. mexicana inopinata* contained widely varying amounts of stored food, as described in the following paragraphs. The stores at seven of the dens were almost entirely of foliage cuttings, but at the eighth den there were only cactus joints and a few acorns.

Den 490810-5 contained approximately a quart of piñon cuttings with needles uneaten. They were scattered among twigs and other food litter and seemed to have been only a diurnal, not a seasonal, food supply.

In den 490819-1 there were one to two quarts of green cuttings lying on the floor of the highest level of living chambers. The cuttings consisted mostly of mountain-mahogany, with lesser amounts of juniper and piñon and a still smaller amount of serviceberry.

The abundant food debris at den 490831-2 contained cuttings and remains of 19 species of plants, 3 more than I recognized growing in the vicinity. But a storage supply amounting to more than a bushel, filling one of the rock clefts of the den, contained only green cuttings of scrub oak. An older store of brown cuttings filling a lower crevice was of more mixed composition with squaw-apple predominating. The older store appeared to have been gathered the previous year.

Den 491024-4 was a house of twigs and debris piled around the base of a clump of skunkbush against the side of a large boulder. Most of the upper and outer spaces of the house were filled with stored food cuttings crammed in tightly. More than a bushel was pulled out as the house was dismantled. More than two thirds of the stored cuttings were skunkbush, with alder next in abundance, and smaller quantities of mugwort, Rocky Mountain juniper, scrub oak, chokecherry, *Clematis ligusticifolia*, *Mirabilis oxybaphoides,* and *Gaura coccinea.* Most storage spaces were filled with masses of the same kind of food crammed in together.

Den 491024-6 contained a small amount of food that might be considered storage, consisting of numerous scattered joints and pieces of rat-tail cactus and some acorns of scrub oak. This supply was probably for diurnal use, primarily.

Den 491024-7 contained a large quantity of stored food consisting of cuttings of mugwort, scrub oak, globe mallow, skunkbush, chokecherry, and goldaster, listed in order of abundance.

Vertical crevices at den 491102-3 were stuffed with approximately two gallons of cuttings. These were mostly of saltbush, some of sagebrush, and a few of Utah juniper.

Den 491116-3 contained an astonishingly large storage supply. There were at least five bushels of scrub oak cuttings with a few cuttings of ponderosa pine and Rocky Mountain juniper mixed in. The cuttings were packed tightly in a large diagonal cleft 8 to 12 inches wide and approximately ten feet long, filling it to a depth varying from 1 to 2½ feet.

At each of the eight dens containing stored food as described above, a rat of this species was trapped and the den was studied in detail. In addition, in a hurried survey of dens at which *no* rats were trapped, five food stores were briefly examined two miles northeast of Bondad on 28 October 1953. These stores are attributed to the Mexican wood rat with reasonable certainty because of the scarcity of cactus spines and the general resemblance to the food materials at other dens of this species (see p. 433, dens 491024-4, 491024-6 and 491024-7). The five food stores were as follows:

(1) A pile of foliage cuttings in a rock cleft contained mostly scrub oak and skunkbush, with some cuttings of chokeberry, *Chrysothamnus nauseosus,* and *Juniperus scopulorum.* There were also a few thistle leaves and one basal clump of grass. (2) A large house on top of a boulder under cottonwood trees was composed of small sticks, twigs and food litter, mostly of scrub oak and skunkbush. At least a bushel of foliage cuttings was piled on top, including large amounts of scrub oak, skunkbush, and two kinds of cottonwood *(Populus angustifolia* and *P. wislizeni).* There was a single rose cutting. (3) A low sandstone cliff was pitted with erosion holes, some of the larger of which were utilized as storage chambers by this wood rat. A few of the lower holes that I could reach had been stuffed with approximately half a bushel of cuttings, mostly of scrub oak and globe mallow, with less of skunkbush and a few of mugwort. (4) This den contained approximately half a bushel of cuttings consisting mostly of scrub oak, with a large amount of globe mallow and some chokecherry, goldaster, skunkbush, and *Chryothamnus nauseosus.* There were a few flower cuttings of sagebrush. (5) A big den in crevices among fallen rocks contained a large mass of old brown twigs nearly filling a large crevice. On top of this mass was approximately a bushel of nearly fresh foliage cuttings. Most of this store was made up of scrub oak and gray saltbush, with some goldaster. There were a few cuttings of sagebrush and of juniper, and one each of piñon, snakeweed, and goosefoot.

REPRODUCTION AND YOUNG

A second year adult female *N. m. fallax* from Boulder County, 7000 feet, taken on 26 June 1935, contained two embryos. Cary (1911: 118) reported a female with three small embryos taken on 1 May at Loveland. He also reported his observation near Boulder of a live female dragging two suckling young on 23 July 1906. I trapped five adult and subadult females in August and September, none of which was in breeding condition.

The reports by Warren (1926: 98) of females of *fallax* in breeding condition all pertain to specimens now referred to other subspecies, and are included in the accounts of *N. m. inopinata* and *N. albigula brevicauda* of the present report.

A subadult was taken on 30 June 1890 at Canon City. A young subadult was taken on 23 July 1948, 3½ miles west of Loveland, 5030 feet. Subadults were collected 7 miles north and 4 miles west of Castle Rock, 6400 feet, on 4 August 1948. Specimens of the immature age class were collected near Gold Hill on 18, 19, and 20 August 1895. Subadults were taken in the same area on 23 July 1906, on 19, 20, and 21 August 1895, and on 10 October 1903. Subadults were also collected 3 miles north of Colorado Springs, 6000 feet, on 20 September 1904, 11 October 1904, and 9 November 1905.

The evidence from reproducing females and young specimens shows that the breeding season extends from late spring through late summer. There is no proof of more than one litter per year for the same female, but the length of the breeding season allows ample time for two litters.

A subadult male, almost adult, taken on 4 August 1948, 7 miles north and 4 miles west of Castle Rock, 6400 feet, had scrotal testes 8 mm long. This rat may have been reproductively active. A first year adult male taken on 21 November 1949, 2 miles east and 1 mile south of Gold Hill, 7100 feet, had abdominal testes 12 mm long. This rat was probably not reproductively active, the mating season probably having ended before November.

All six females of *N. m. scopulorum* trapped by me in May and early June were in breeding condition, as shown in Table 19, indicating that litters are born in late spring and early summer. A subadult rat was taken on 11 April 1918 at Regnier, showing that young are also born in early spring. Two and three young per litter seem to be the normal numbers.

A female *N. m. inopinata* from Bondad was pregnant and recently lactating on 15 June 1949, indicating that two litters are sometimes

TABLE 19.—BREEDING CONDITION OF FEMALES OF N. M. SCOPULORUM

LOCALITY	Date	Age	Weight	Condition
Two Buttes Reservoir, 4200 ft.	9 May	2nd year adult	246 g	3 embryos 16mm
Two Buttes peak, 4600 ft.	9 May	3rd year adult	231 g	3 embryos 8 mm
3 mi. NW Higbee, 4300 ft.	15 May	2nd year adult	187 g	2 embryos 46 mm
3 mi. NW Higbee, 4300 ft.	15 May	2nd year adult	161 g	2 embryos 8 mm
Regnier, 4500 ft.	30 May	3rd year adult	201 g	lactating, 2 scars
Regnier, 4500 ft.	2 June	2nd year adult	192 g	lactating

TABLE 20.—BREEDING CONDITION OF FEMALES OF N. M. INOPINATA

LOCALITY	Date	Age	Weight	Condition
Coventry, 6800 ft.	9 April	2nd year adult	....	2 large embryos
Bondad, 6050 ft.	15 June	2nd year adult	177 g	recently lactating, 2 embryos 17 mm
Bondad, 6050 ft.	15 June	2nd year adult	159 g	recently lactating, no emb.
Bondad, 6050 ft.	15 June	subadult	115 g	3 scars 8 mm
1 mi. SW Gateway, 4600 ft.	19 June	2nd year adult	168 g	lactating, no embryo
1 mi. SW Gateway, 4600 ft.	19 June	2nd year adult	175 g	lactating, no embryo
1 mi. E Naturita, 5900 ft.	26 June	3rd year adult	202 g	lactating, no embryo
4 mi. W, 2 mi. S Cahone, 7000 ft.	1 Aug.	2nd year adult	178 g	nipples drying up, no emb.
* Cortez, 6200 ft.	4 April	....	....	lactating
* Sieber Ranch, 5675 ft.	12 May	....	....	4 large embryo

produced by one female in the same year. Six out of nine subadult and adult females taken in June were in breeding condition. The only subadult was pregnant. Thirteen other subadult and adult females taken from early August through early November were neither pregnant nor lactating. The females indicated by asterisks in Table 20 were reported by Warren (1926: 98) under the name *Neotoma mexicana fallax.*

Immature and subadult specimens from many localities in southwestern Colorado, support the evidence of breeding season presented in the above table and extend the record into early fall. An immature rat from two miles east of Durango, 7500 feet, weighed 66 grams on 10 September 1949. Two suckling juveniles, one of which weighed 15 grams, were found at the Rangers' Quarters, Mesa Verde National Park, on 2 September 1949. It seems that litters are born in the months April through August at least. There are 2 to 4 young per litter.

TABLE 21.—BREEDING CONDITION OF MALES OF N. M. INOPINATA

LOCALITY	Date	Age	Weight	Condition
Bondad, 6050 ft.	15 June	2nd year adult	158 g	testes scrotal
Bondad, 6050 ft.	15 June	2nd year adult	168 g	testes scrotal 19 mm
1 mi. SW Gateway, 4600 ft.	19 June	2nd year adult	194 g	testes scrotal 21 mm
1 mi. E Naturita, 5900 ft.	26 June	3rd year adult	191 g	testes scrotal
1 mi. N Cahone, 6900 ft.	2 Aug.	1st year adult	130 g	testes scrotal
4 mi. W, 2 mi. S Cahone, 7000 ft.	2 Aug.	1st year adult	154 g	testes scrotal

MOLTS

The patterns of molt in *N. mexicana* are much like those of *N. cinerea,* as described in some detail under that species (see p. 398). The postjuvenal and second molts show a few minor differences from the patterns of these molts in *cinerea.* The molt of the inguinal region is less delayed in *mexicana* than in *cinerea* but not usually so early as in *N. floridana* and *N. micropus.* Molt lines from the sides of the body join on the lumbar region and rump at almost the same time, before they have quite joined at the base of the tail. There is usually a third molt in the first year, as occurs also in *cinerea.* The third molt was recognized in specimens taken in the period September through January, and only in adults of about five to eight months age. The third molt begins on the belly, at least sometimes, before completion of the second molt on the head, and progresses in the same pattern as the second molt. In characteristics of molt, *N. mexicana* seems to stand somewhat between the other round-tailed wood rats and the bushy-tailed wood rats but closer to the former.

Brief descriptions of some specimens in order of age are given below in order to illustrate significant stages in different molts and to show differences from the basic pattern described in more detail for *N. cinerea.* The seasonal distribution of specimens in molt is shown in Plate 22.

DMNH 755, immature male *inopinata* from Ute Peak, 5 June 1913, shows the postjuvenal molt on the inguinal region unusually well because of the old style in which the skin was put up, with the hind legs and tail extended in natural attitudes. Subadult hairs are full grown on the abdomen and half grown on the sides. The groins are covered with a "stubble" of new hair-tips overlain by long fine juvenal hairs. Short hairs have appeared on the breast forward to the level of the ears and over the lower half of the back, except at the base of the tail.

A subadult female *fallax* (KU 29187) from 7 miles north and 4 miles west of Castle Rock was in postjuvenal molt on 4 August on the shoulders and middle of the back and in a small patch at the base of the tail. New pelage covers the entire belly, inguinal region, sides, and rump.

The postjuvenal molt is more advanced in ERW 282, subadult male, from Colorado Springs on 20 September. Short hairs are concealed between the shoulders, over the entire throat, and up over the cheeks and sides of the snout. Another rat (ERW 4120) with molt well advanced on the back and throat has a separate patch of new subadult pelage on each side of the rostrum and extending back to a line below each eye.

A subadult male *scopulorum* (DMNH 1888) from Regnier, 4 November, shows two molts at once. There is postjuvenal molt between the shoulders, with juvenal pelage remaining on the nape and crown, while the second molt is well started on the middle of the belly.

KU 29183, subadult male, from 7 miles north and 4 miles west of Castle Rock, taken on 4 August, is in the second molt with the first autumn pelage growing in thickly on the sides and flanks. BSC 148009, subadult female, from Gold Hill, 23 July, has the second molt more advanced. Both KU 29183 and BSC 148009 have distinctly bicolor tails with hairs as long and straight as in second year adults. This fully mature appearance of the tail seems to have been acquired with the postjuvenal molt.

A first year adult female (BSC 129813) from Gold Hill, 8 October 1903, reveals two molts in progress at once. The first assumption, that these are the postjuvenal and second molts, is untenable, for all the morphological evidence as to the age of the rat and identity of the pelages points to the conclusion that the two molts present are the second and third molts of the year. The earlier molt can be seen on the nape and between the shoulders, where the short new hairs are covered by older pelage. A molt line separates the older pelage on the nape from full new pelage covering the crown and face. Posteriorly on the back and sides the new pelage reaches full length but is not sharply set off from the older pelage on the nape and upper back. The older pelage is a little grayer than the newer pelage covering most of the body, but does not have the fine soft texture and grayness of juvenal pelage. The later molt can be seen in a marginal band around the abdomen. The band of short concealed hairs crosses the lower breast and runs down each side at the lateral line onto the thighs. On the insides of the thighs the lines double back forward to cross the venter in front of the inguinal region. The abdomen is in full new pelage (the fourth pelage of the year) that is referred to in this work as the first winter pelage. Isolated patches of short hairs on the rump and lumbar region also represent the first winter pelage. The tail is sharply bicolor, indistinguishable from that of a second year adult. The skull is in all respects referable to the first year adult age class. Comparison of the skull with that of BSC 148009 reveals that BSC 129813 is clearly the older, as indicated by the greater wear on the teeth, the closed exoccipital sutures, and greater ossification of the maxillary branch of the zygoma.

The second and third molts seem to have been in progress also simultaneously on ClMNH 10627, first year adult female *fallax,* from three miles southwest of Colorado Springs on 15 November.

KU 34815, first year adult female *inopinata,* from 2 miles west and 1 mile south of Chromo on 16 November, seems to be in a late stage of the third molt.

ERW 1443, adult female, from Ashbaugh's Ranch, 10 April 1906, is in molt on the belly and on the head and has a few small tufts of new hairs scattered on the dorsum. Although the skull of this specimen is missing, the worn adult pelage could not be that of a first year rat. The condition of the nipples indicates that the rat had been lactating. This specimen is the earliest seasonal record of the annual molt and shows that even females with young may molt as early in the year as males.

Irregular annual molt was in progress beneath the old, rough reddish pelage on nearly all the upper parts of ClMNH 12320, second year adult male, from ten miles south of Colorado Springs, taken on 6 September. Molt had been completed on the belly.

The annual molt of an old adult female *inopinata* (KU 34808) from two miles northeast of Bondad, 24 October 1949, is nearly completed and seems to have progressed in a more regular fashion, like that of the early molts. The venter, sides, legs, and lower back are in full new pelage. On the upper back there is a lop-sided V-shaped pattern of molt, the left arm forming a thin molt line and the right arm spreading over a broad area. There is also a molt line across the crown. The old pelage on the nape and upper back looks to be nearly as fresh and unworn as the new pelage.

PARASITES

The kinds of parasites collected from Mexican wood rats in the present study and the field numbers of individual hosts are listed below for each subspecies of wood rat.

Neotoma mexicana fallax:

Ixodidae

Dermacentor andersoni, 480804-6 (1 nymph)
Ixodes spinipalpis?, 480804-1 (1 nymph)

Laelaptidae

Eviphis sp., 480804-1

Trombiculidae

Trombicula (Eutrombicula) alfreddugesi, 480708-1, 480804-1, 2, 5 & 6, 480916-2, 480917-1
Trombicula (Neotrombicula) harperi, 480804-1, 2, 5 & 6

Hystrichopsyllidae

Megarthroglossus sp., 480917-1

Ceratophyllidae

Diamanus montanus, 480804-5
Orchopeas sexdentatus, 480804-6, 480916-2

Neotoma mexicana scopulorum:

Hystrichopsyllidae

Stenistomera alpina, 500509-1

Neotoma mexicana inopinata:

Taeniidae

Taenia sp., 490621-3 (larva)

Ixodidae

Dermacentor andersoni, 490801-4 (1 nymph and 3 larvae), 490810-4 (1 nymph)
Ixodes spinipalpis, 491024-7 (1 ♀)
Ixodes woodi, 491024-7 (1 nymph)

Laelaptidae

Eubrachylaelaps circularis, 491106-4
Haemolaelaps glasgowi, 490615-1

Macronyssidae

Hirstionyssus cf. *H. otomys,* 491106-4

Trombiculidae

Leeuwenhockia americana, 491106-4
Euschöngastia criceticola, 491106-4, 491116-3
Euschöngastia lacerta, 490802-4
Euschöngastia hoffmannae, 490802-4
Euschöngastia finleyi, 491106-4

Trombicula (Eutrombicula) alfreddugesi, 490801-4
Trombicula hoplai, 490810-1 & 4 (from New Mexico)
Trombicula potosina, 490619-4 & 5, 490801-4, 490802-4, 490810-1 & 4

Haematopinidae

Neohaematopinus inornatus, 490615-1, 490801-4

Reduviidae

Triatoma protracta, 490621-3

Hystrichopsyllidae

Anomiopsyllus sp., 490615-1, 490802-3
Stenistomera alpina, 491116-3

Ceratophyllidae

Diamanus montanus, 490802-3
Malaraeus sp., 490615-1
Orchopeas sexdentatus, 490619-5, 490802-2, 490802-4, 490810-1
Peromyscopsylla sp., 491116-3

INJURIES AND DISEASE

An adult female (ClMNH 11174) from ten miles south of Colorado Springs, taken on 25 December 1936, has an alveolar abscess between the first and second right upper molars. The bony pit extends one third of the distance across the palate and measures 3.9 mm in diameter from the outer (labial) to the inner (lingual) rim. The posterior surface of the first molar and anterior surface of the second molar, both of which show some enamel wear from contact, are now 0.5 mm apart. The first molar has been displaced forward and outward from the tooth-row, probably by lodgement of cactus glochids (bristles) or other foreign material in the inner side of the alveolus where the pit is largest. Neither of the teeth adjoining the pit show any decay, though the roots are deeply exposed. The diastema on the right side is 11.9 mm and on the left side 12.3 mm. The molar tooth row is 9.4 mm long on the right and 9.1 mm long on the left side. The first and second left upper molars are in contact and normal. The pelage of this rat has a smooth healthy appearance. A similar alveolar deformity in *N. albigula* is described on page 486.

The type specimen of *N. m. scopulorum* from three miles northwest of Higbee has a large alveolar abscess surrounding the abnormal first left upper molar. The molars are in an advanced state of wear with only slight depth of enamel remaining. There are two, much worn, peglike fragments of the first upper molar projecting slightly from an ovoid alveolar cavity 5.1 mm long and 4.3 mm wide. As a result of the reduction of wear on the opposing first lower molar, the crown of the lower molar is much less worn than those of the other lower molars and projects 0.8 mm above the occlusal level of the two posterior molars. A few cactus glochids (barbed bristles) are imbedded in the cavity around the base of the molar remnants. Although glochids are of rather frequent and normal occurrence between the teeth of *Neotoma albigula* and *N. micropus,* they are not so commonly found in *N. mexicana* and possibly induced the alveolar infection in this individual.

Neotoma albigula Hartley

White-throated wood rat

HABITAT

The white-throated wood rat lives in climatic conditions ranging from extreme desert in southern Arizona and Mexico to hot semi-arid in the Colorado Plateau Province and the Southern Great Plains. The species endures a moderately cold winter with snow and occasional blizzards in these more northerly parts of its range, including southwestern and southeastern Colorado. The upper zonal limit of *albigula* is somewhat below the upper limit of the Upper Sonoran Life-zone. At locations in Colorado with southerly exposure this limit is close to the 7000 foot level but undoubtedly varies from year to year. There seems to be no significant difference in climatic tolerance between the subspecies *brevicauda*, *laplataensis*, and *warreni*, insofar as can be judged by their altitudinal occurrence. The upper limit of *N. albigula* is probably controlled primarily by low temperature, or a combination of climatic factors.

In western Colorado *N. albigula* nearly always occurs in either the piñon—juniper woodland or the juniper—sagebrush scrub community. In both these communities one or more species of prickly pear cactus is numerous, sometimes growing in large clumps. These cacti of the genus *Opuntia* are regularly used in great quantities for food and shelter. Juniper is also frequently used both for food and building material and is probably second only to cactus in importance for *N. albigula*. The piñon is much less important than juniper, and sagebrush is eaten only in trivial amounts, although the sticks of both are used commonly for shelter. *N. a. brevicauda* and *laplataensis* occupy the same plant communities and seem to have the same preferences for cactus and juniper.

In southeastern Colorado *N. a. warreni* likewise has a strong dependence on cactus and junipers for food and shelter. However, *warreni* occurs in a somewhat different set of plant communities, in comparison with the two western subspecies, because of differences in the communities and kinds of plants available. The tree cactus, which occurs in the range of *warreni*, has a growth form distinctly different from that of any cactus of western Colorado and is a major component in some of the communities favorable for *warreni*. The tree cactus seems to be preferred by *warreni* over any of the common species of prickly pear, probably because it provides better material and support for house building. It is most abundant on alluvial fans as part of the tree cactus—short grass community, but it occurs also on rocky hillsides as part of the juniper—tree cactus community. *N. a. warreni* is a regular inhabitant of the latter community but occupies the tree cactus—short grass community usually only in the absence of *N. micropus.* On the eastern edge of its range, outside of the range of the tree cactus, *warreni* occurs in the juniper—yucca, yucca—skunkbush, and yucca—short grass communities, which do not occur in western Colorado.

The numbers of dens examined in each kind of plant community, all in the Upper Sonoran Life-zone, are presented in Table 22 for each subspecies.

TABLE 22.—PLANT COMMUNITIES OF N. ALBIGULA

COMMUNITIES	Numbers of dens		
	N. a. brevicauda	*N. a. laplataensis*	*N. a. warreni*
Piñon—juniper	....	9	1
Juniper—sagebrush	7	3	....
edge Sagebrush and Mixed shrub	....	1	....
Juniper—tree cactus	....	....	3
Cottonwood—juniper—tree cactus	....	....	1
Tree cactus—short-grass	....	....	4
Juniper—yucca	....	....	4
Yucca—skunkbush	....	....	3
Yucca—short-grass	....	....	1
Short-grass—scattered juniper	....	....	2
Totals	7	13	19

Shelter used by the white-throated wood rat is of two general types, natural rock dens to which more or less spiny debris may be added, and dome-shaped houses of various debris heaped up about the base of a shrub or clump of cactus. The kinds of rock shelter selected are nearly always at the ground level, rather than high up on cliffs or large caves. Dens are more frequently in horizontal crevices and under low rock ledges than in vertical clefts. Dens are almost as commonly situated under boulders or large fallen sandstone blocks. Although abandoned buildings may occasionally be occupied, this species seems less inclined than *cinerea* and *mexicana* to use man-made shelter. The ability of *albigula* to construct houses in the open enables it to occupy valley bottoms, alluvial fans, and other terrain of low relief where cactus is numerous. Rock dens are usually used on canyon sides, steep hillsides, and along the bases of cliffs. The occupancy of rock dens or cactus houses in eastern Colorado seems to be determined not so much by availability or preference as by the presence or absence of *N. micropus* in the same area. (See p. 531 for discussion of competition between these species.)

The numbers of dens examined in each kind of shelter and in each kind of topography are presented in Table 23. Double prime digits refer to *N. a. brevicauda*. Prime digits refer to *N. a. laplataensis*. Plain digits refer to *N. a. warreni*.

TABLE 23.—SHELTER AND TOPOGRAPHY OF N. ALBIGULA

	Topography and number of dens									
SHELTER	Cliff base on steep slope	Cliff base by valley floor	Steep rocky slope	Low rocky rim of small valley	Moderate rocky slope	Bottom of wash on moderate slope	Gentle valley slope	Creek bank on valley floor	Gently rolling High Plains	Totals
Vertical rock crevice	....	1″	....	....	....	....	....	....	....	1
Vertical and horizontal crevices and overhang	....	1″	....	....	....	....	....	....	....	1
Horizontal cleft under sandstone outcrop	....	....	3′	2′	1′	....	1″ 2	....	....	9
Several boulders	....	....	1′	....	2	....	....	....	....	3
Big rock block	1″	....	3′	....	2′ 1	....	1′	....	....	8
Hollow trunk of cottonwood tree	....	....	....	....	....	....	....	1	....	1
House among boulders and sage bushes	....	....	....	....	....	....	1″	....	....	1
House in clump of skunkbush	....	....	....	....	1	....	1	1″	....	3
House in felled juniper and clump of saltbush	....	....	....	....	....	....	....	1″	....	1
House in juniper	....	....	....	....	3	1	....	....	2	6
House in tree cactus	....	....	....	....	....	....	4	....	....	4
Tunnels under clump of yucca	....	....	....	....	....	....	....	....	1	1
Totals	1	2	7	2	10	1	10	3	3	39

Wherever in Colorado *N. albigula* occurs, it may encounter also one or more other species. At some localities there is habitat separation, more or less distinct, between the species, but more often they occur in the same habitats. Optimum habitat conditions for each species are more easily recognized where there is habitat separation. An instructive example of this situation was studied in the lower Dolores Canyon near Gateway where both *N. a. brevicauda* and *N. m. inopinata* were abundant in 1949.

The canyon of the Dolores River between the La Sal Mountains and the Uncompahgre Plateau is more than 2000 feet deep including a steplike series of cliffs. The inner canyon varies in width from a narrow gorge to a valley bottom more than a mile across. The bottom at Gateway is bordered by alluvial fans and terraces dissected by tributary creeks. At the mouth of John Brown Creek, one mile southwest of Gateway, 4600 feet elevation, and on the west side of the Dolores River northward, the fans and terraces consist of coarse gravels, reddish sands, and silts. Large boulders lie scattered over the surface in some areas. The lowest clifflike outcrop is composed of purplish sands and conglomerate, the Shinarump formation, above which lies a talus-strewn slope of soft red sands and shales of the Chinlee formation. At the top of the slope stands an imposing wall of cliffs, formed by the Wingate sandstone, which is the principal sheer cliff-forming rock of Dolores Canyon. The Wingate cliffs are angularly broken by many vertical joints and crevices offering an abundance of shelter for any small animals able to scale the heights. The next higher level of major cliffs is formed by the Entrada formation, a yellowish massive sandstone presenting smoothly rounded surfaces with few crevices. In some places the Entrada forms steep slopes partly wooded with piñons and junipers. Above the Entrada still-higher cliffs are formed by the reddish Morrison formation and the gray Dakota sandstone. Above the Dakota is a broad nearly flat upland at 7300 feet elevation extending westward to the flank of the La Sal Mountains.

The principal shrub on the valley bottom and alluvial fans was sagebrush. Two kinds of prickly pears *(O. phaeacantha* and *O. polyacantha)* were nearly equally abundant, but the bunchball cactus and Devil's claw cactus were scarce. No greasewood was seen near John Brown Creek but it was abundant a few miles north on low silty bottomland where the soil was more alkaline. The dominant shrub on the steep slopes was the Utah juniper. At high elevations on the canyon sides and on the upland mixed piñons and junipers of larger size were abundant. On the alluvial terrace four miles northwest of Gateway, junipers, sagebrush, and blackbush were numerous, and the most abundant cactus was *O. rhodantha.*

On the valley floor at the mouth of John Brown Creek the white-throated wood rat occupied dens made of large piles of sticks, stock manure, and cactus debris. These were erected among small boulders or at the base of a bush or thicket or on a fallen juniper trunk. On the edge of the valley bottom both the white-throated and Mexican wood rats had dens in similar rock shelters, usually low horizontal crevices at the base of a cliff or steep slope or under sandstone talus blocks. Similar dens higher up the steep slopes seemed to belong only to the Mexican wood rat. Ascending John Brown Canyon I saw no sign of *N. albigula* above 5000 feet elevation, although cactus was seen growing at least as high as 5800 feet, and probably occurs considerably higher. A Mexican wood rat was trapped at a den in crevices in a cliff near the canyon bottom at 5500 feet.

Several houses of sticks, manure, and cactus spines were seen on the lower edge of the alluvial terrace four miles northwest of Gateway. They utilized the shelter of junipers and large sandstone blocks. Although no rats were obtained, the dens could only have been made by *albigula*. No dens at all were seen on the silty bottomland covered with greasewood and some cactus, probably because of the absence of both rocks and junipers for shelter.

The bushy-tailed wood rat also occurs in Dolores Canyon near Gateway, but seemingly only at higher elevations in the cliffs. Although I drove up John Brown Canyon to the flat at 7300 feet and set a few traps on the way back down, I obtained no *N. cinerea* and saw only a few dens of doubtful ownership. However, Mr. Lyman Hubbard, rancher, on whose land I camped, related that he knew of two kinds of rats, a smooth-tailed rat living in the canyon bottom and a bushy-tailed rat living higher up in the cliffs and mine tunnels. (He was interested to see the two round-tailed species I showed him from the canyon bottom and lower slopes.) He did not recall ever seeing the bushy-tailed wood rat below the upper part of the Wingate, but he had seen it on up in the Entrada, Morrison, and Dakota formations and in the "cedars" on top. This local range agreed fairly well with my expectations except that any level in the Wingate, even the base between 5500 and 6000 feet, appeared to have plenty of excellent crevices. In contrast, deep vertical crevices were scarce in rocks below the Wingate. Mr. Hubbard, who had lived many years in the Gateway area, had a strong appreciation of nature and outdoor life. I judged him to be a keen and intelligent observer with a good memory for details.

In Mancos Canyon south of Mesa Verde (6 miles east and 17 miles south of Cortez, 5600 feet) dens of *N. a. laplataensis* and *N. m. inopinata* were numerous, *laplataensis* perhaps being the more common of the two species. Mancos Canyon is broadly rounded, with cliffs of Mesa Verde sandstone outlining the highest level. The vegetation of the alluvial slopes is of fairly scattered but numerous Utah junipers and fewer piñons, with a ground cover of abundant sagebrush and shadscale. Higher up on the talus slope matrimony vine, mountain-mahogany, serviceberry, *Yucca baccata*, and Mormon tea are more numerous. On the silty bottomland grows a tall dense stand of greasewood, and along the river bank, willows. Three kinds of prickly pear cacti and bunchball cactus were widespread on the talus slope and alluvial fans but scarce on the bottomland.

Wood rat dens were either in outcrops of sandstone bedrock on the steeper slopes, or under larger fallen blocks of sandstone there or on the upper edge of the alluvial fans. Although I crossed the bottomland three times I found no sign of wood rats, probably because of the scarcity of boulders and cactus there. I saw no stick or cactus houses of any sort in Mancos Canyon. *N. albigula* dens were more numerous than those of *mexicana* under large talus blocks, whereas dens of *mexicana* seemed to be more numerous in ledge crevices of bedrock and cliffs. But there was little, if any, real habitat separation. It is probable that *N. cinerea arizonae* lives in the higher cliffs of Mesa Verde sandstone bordering Mancos Canyon. *N. cinerea* and *N. mexicana* live in the same sandstone cliffs and caves in the tributary canyons of Mesa Verde, where Pueblo cliff dwellers lived in the thirteenth century, A. D.

Although no specimen of *albigula* was obtained on the rim of Cahone Canyon, a single unmistakable cactus spine midden there indicates that the habitat, described on page 362, is suitable for *albigula* but probably at the upper limit of its zonal range. For a description of this den and cactus midden see page 461. *N. albigula laplataensis* lives in the same habitat with *N. m. inopinata* at Bondad. Habitats there and along the Florida River, two miles north of Bondad, are described on page 412 under the account of *mexicana*.

Numerous dens of *N. albigula* among rocks were examined in the valley of Cherry Creek, 5 miles east and 15 miles south of Mancos. They were at elevations between 6500 and 7000 feet. At higher elevations farther up the valley no dens of this species were found, only those of *N. mexicana*. Since the topography, rock outcrops, and vegetation are essentially similar above and below the 7000 foot contour in Cherry Creek valley, temperature seems to be the most likely factor determining the upper limit of occurrence.

The valley cuts through the upland sloping southward from the foot of the La Plata Mountains. It is small with low sides and a narrow flat bottom which is in some places wide enough for a small farm. The eastern rim of the valley is shown in Plate 30, Figure 1. All dens of *albigula* were in horizontal crevices under overhanging rock ledges. The dominant vegetation was scattered Utah junipers and piñons on the upper slopes and above the rim. The lower slopes and flats were mostly covered with sage brush. Along the creek grew narrowleaf cottonwoods, willows, chokecherry and scrub oak thickets. Six species of cactus were recognized. They were most abundant above the rim. Farther up the valley at 7000 feet elevation and higher the junipers and piñons were larger and closer together. Dens of *N. mexicana* were found among the same rocks but were less numerous below 7000 feet.

In southeastern Colorado the Purgatoire River has cut a relatively broad valley through the upland surface of the High Plains. The rim of the valley is rocky and abrupt, formed by the resistant Dakota sandstone. At Higbee the valley is approximately a mile wide and 300 feet deep. The tree cactus grows abundantly on the alluvial fans bordering the valley bottom and more scattered on the steeper rocky slopes and the upland. Scattered one-seed junipers grow on the rocky slopes and on the upland near the rim. Other conspicuous plants are soapweed, skunkbush, saltbush, *Opuntia humifusa*, and *O. polyacantha*. Short grasses and low forbs are the principal ground cover everywhere. Numerous cactus houses of *N. a. warreni* were examined in 1950 in tree cacti on the alluvial fans north of the river. Houses of sticks and cow chips were situated in some of the junipers on the rocky slopes and valley rim, and one was in a clump of skunkbush. Dens of this species were seen also among rocks on the rim and steeper slopes. Two dens were in hollow cottonwood trees on a creek bank.

The only other species of wood rat obtained near Higbee was *N. m. scopulorum,* which had dens under rock ledges and boulders along the valley rim, but none on the alluvial fans where *warreni* was most numerous.

In similar topographic and vegetational conditions, described on page 487, *albigula* occupies rocks and junipers but is replaced by *micropus* in the tree cactus. *N. albigula* and *micropus* both occurred in rock dens in upper Chacuaco Canyon described on page 488.

In nearly every habitat where *N. albigula* was obtained, at least one or more species of *Opuntia* cactus was abundant. However, in the vicinity of Two Buttes *albigula warreni* was the commonest kind of wood rat in 1950 although cactus of any kind was scarce. The tree cactus did not occur so far northeast as Two Buttes, and the prickly pears (*O. humifusa* and *O. polyacantha)* grew only widely scattered in small clumps or as single plants. In the vicinity of Two Buttes *warreni* subsisted mostly on juniper and soapweed instead of on cactus.

The twin summits of Two Buttes rise some 150 feet above the gently rolling High Plains. Two miles south of the buttes the valley of Two Buttes Creek has been dammed to form a reservoir. Below the dam is a shallow canyon formed by low cliffs of Dakota sandstone on each side of the valley floor.

Dens of *albigula* were under and among broken rocks on the lower slopes of Two Buttes where the principal vegetation was skunkbush, soapweed *(Yucca glauca),* and grasses. Near the top of the peak, where skunkbush was most abundant and soapweed scarce, dens of *mexicana* were among loose rocks derived from the caprock and underlying outcrops. (See page 412.) The grazed short-grass plains around Two Buttes were speckled with soapweed, which was widely scattered on the highest surfaces and abundant in a low area at the head of a tributary leading south into Two Buttes Reservoir. *N. albigula* and *micropus* lived in the larger clumps of soapweed, where their dens consisted of low mounds of livestock manure and weed stalks among the spiny heads of soapweed, and burrows under the roots in the fine soft soil. On the upper slopes of the next tributary valley leading east to Two Buttes Creek there were a few scattered one-seed junipers; a large proportion of these provided shelter for houses built of sticks and cow chips. All specimens obtained from these houses were of the species *albigula.*

DENS

The white-throated wood rat is as much a house builder as a rock dweller, but in any given part of its range lives mostly or solely in one or the other type of den. The type seems to be determined partly by availability and partly by competition with the gray wood rat. (See pages 531 to 533.) In Colorado, *albigula* commonly inhabits rock dens but builds many houses in a few local areas. Although houses, because of their diversity, received a large proportion of my attention, they were greatly outnumbered by dens under rock ledges and fallen blocks, which received only brief notice because of their uniformity and the inaccessibility of their interiors.

In western Colorado houses were seen only in lower Dolores Canyon near Gateway. The type series of the same subspecies *(brevicauda)* was collected by Durrant and others from houses on the floor of Castle Valley, Utah. Farther south I found no houses in Colorado made by *laplataensis,* but Kenneth Ross told me that formerly there were wood rat houses in the region of Cahone Canyon. Ross, as a youth, used to ride over the mesas on horseback in the early thirties. He saw a number of large houses of wood rats built around junipers, sagebrush, and clumps of yucca on the mesa top, well back from canyon rims. He saw a house 2 to 3 feet high at the site of the Pueblo surface ruin four miles west and two miles south of Cahone. I searched the area pointed out by Ross and made several transects of two mesa tops without finding a trace of a house, although rock dens were numerous along the canyon rims. It was evident that dens of *albigula* among rocks were rare, compared with those of *cinerea* and *mexicana.* Since that locality was marginal for *albigula,* perhaps the population fluctuates greatly and occupies houses on the mesas only in more favorable years. Ross saw also some stick houses in the southern part of Mesa Verde National Park while he was serving as Park Naturalist. Since all these houses had much cactus debris, and no other species of rat in the region is known to build such houses, they probably had been made by *albigula.*

In eastern Colorado houses were seen at several localities, and rock dens were seen at most of the same localities and at some others. Although houses possibly outnumber dens of *albigula* in the piñon—juniper country between the foothills of the Rockies and the western limit of *micropus,* the impossibility of distinguishing houses of these species without identifying the owner makes any passing visual survey unreliable.

Rock dens of *albigula* are characteristically under large boulders or talus blocks or under projecting rock outcrops. The unifying physical features of these two kinds of rocks are horizontal clefts or spaces on or close to the ground level. Rarely *albigula* will occupy vertical or diagonal clefts to a height of six feet above the ground. The preference for low horizontal clefts seems to be a real one by which *albigula* is adapted to use the most abundant rock shelter within its range. However, this conclusion could not be verified in Colorado, because at most localities where other kinds of rock shelter were present these were already occupied by *cinerea,* or less frequently *mexicana.* In such situations competition for den sites could account for the difference. The question could be settled by observation of the distribution of rock dens in relation to available types of rock shelter in southern Arizona at elevations below the ranges of other species of wood rat.

The house of *albigula* is nearly always built around some natural base or support that by its own features determines many of the characteristics of the house. Most common kinds of support are junipers and clumps of cactus. Other shrubs such as sagebrush, skunkbush, and yucca also occasionally support houses. If the house is built on or against a boulder or pile of rocks, the den may be referred to as composite, in that both the natural shelter and the rat-made structure provide protected living space.

There are few, if any, common characteristics of houses of the white-throated wood rat. They are usually low mounds or conical piles of debris rarely two feet high. In my experience the house invariably has more than one entrance. There is usually a large central chamber above ground. Other features vary with the environment. Underground burrows seem to be more frequently absent than present, probably depending on the adequacy of shelter above ground and on the hardness of the soil. The number of levels of chambers and passageways in the den is influenced by steepness of ground slope as well as height of house.

The common junipers used by wood rats in western and eastern Colorado differ in growth form. *Juniperus utahensis* in western Colorado has a distinct trunk for at least a short distance above ground, whereas *J. monosperma* in southeastern Colorado has several or many basal branches leaving the root-crown at or below the surface of the soil. Consequently houses of *N. a. brevicauda* are built against the trunk of *J. utahensis* and are probably seldom high enough to incorporate more than a crotch or two of the lower branches; or a composite house may be built between a large *utahensis* and a boulder. On the other hand, houses of *N. a. warreni* are sometimes built right in the midst of *J. monosperma* where they are screened on all sides by spreading branches and supported by central branches penetrating the house. (See Pl. 32, Fig. 1.) Other houses of *warreni* are built against main stems of *monosperma* and under low arching branches that run through and support the crown of the house. (See Pl. 32, Fig. 2.) The latter condition is especially favorable for the formation of a large central chamber.

Houses supported by cacti were seen only in that part of eastern

Colorado where the tree cactus, a species of cholla, occurs and is the principal support. The rat-tail cactus is the only cholla occurring in western Colorado and is too small a plant to support a wood rat house.

Although one of the larger species of prickly pear in Colorado may occasionally serve as a base for a house when other shelter plants are in short supply, I have not found such a house. The largest kind of prickly pear in Colorado (*O. phaeacantha*) does not grow nearly so high as several species in Arizona, where the prickly pear provides excellent shelter and support for houses of *N. a. albigula* (Vorhies and Taylor, 1940, Plate IV-1).

Houses of *warreni* built in the tree cactus usually have chambers on two levels, a main central chamber with its floor resting on the basal branches that diverge from the stem at the ground level, and an underground trench or ring chamber running around the stem just below the basal branches and above the roots. There is usually a peripheral runway closely encircling the outside of the house. The central chamber seems ordinarily to be used as a feeding place, although the nest is sometimes also located there. Vorhies and Taylor (1940: 484) hesitated to accept the "feeding platform" of Spencer as a characteristic part of the upper structure because they found more evidence on the Santa Rita Experimental Range, Arizona, for feeding below ground. It seems likely to me that Spencer's term was based on houses in a supporting plant such as the tree cactus or one-seed juniper, with a few main branches arising from the ground level, whereas most of the dens referred to by Vorhies and Taylor may have been in the open or under plants of different nature. It is clear from Plate I (*op. cit.*) that the commonly used cholla (*O. fulgida*) with its single erect stem does not provide the same structural framework for a house as does *O. arborescens.*

The white-throated wood rat occasionally uses other kinds of shelter, such as hollow cottonwoods in southeastern Colorado. Cary (1911: 116) found *warreni* living in hollow junipers, as well as rock dens and stick houses, at Gaume's Ranch. Vorhies and Taylor (1940: 464) reported *N. a. albigula* using holes and crevices in cut banks of earth along washes in Arizona, and invading cabins and country houses (*op. cit.*: 467).

Nests of the white-throated wood rat are usually domed or ball-shaped but sometimes only semidomed or semiroofed. I found none that was cup-shaped. A typical ball-shaped nest is between 6 and 10 inches in diameter with a chamber 3 to 4½ inches across.

The location is usually on the ground level, or occasionally on a higher level in a house, but rarely in a chamber or tunnel completely underground. Some nests are partly embedded in the soil and others are embedded in a midden of cactus spines and other food litter that has accumulated around the base of a nest almost up to its mouth.

The availability of soft fibrous material is the determining factor in the selection of nesting materials. In western Colorado shredded

TABLE 24.—MATERIALS ACCUMULATED AT DENS OF N. ALBIGULA

MATERIALS	Number of dens			Totals
	N. a. brevicauda	*N. a. laplataensis*	*N. a. warreni*	
sticks	7	13	14	34
juniper	6	2	9	
sagebrush	4	8		
skunkbush		1	4	
piñon		2		
gray saltbush	1			
pale desert-thorn		1		
cottonwood			1	
unidentified	1	5	2	
cactus joints and cholla sticks	7	13	7	27
Opuntia polyacantha and few *hystricina*	6	6		
O. arborescens			7	
O. rhodantha		6		
O. phaeacantha	5	1		
O. davisii		2		
Echinocactus whipplei	1			
livestock dung	6	7	18	31
bones	4	9	6	19
small stones		2	11	13
dry weed stalks			10	10
yucca stalks and blades			9	9
piñon cones	1	4	1	6
Russian thistle	2		4	6
carnivore scats		2	1	3
feathers			3	3
piece of paper wasp comb	1		2	3
paper	1		2	3
cellophane			3	3
owl pellets			2	2
potsherds		2		2
broken glass			2	2

Each of the following items was present at one den of the subspecies: *brevicauda:* mule deer hair; *laplataensis:* piece of corncob, piece of chicken eggshell, piece of leather, insulated wire; *warreni:* dry goldenrod stalks, dry thistle heads, dried horned lizard, shed piece of snake skin, peach pit, cloth, cardboard, heel of lady's shoe, piece of inner tube, tinfoil, bottle cap.

bark of the Utah juniper is most abundantly used, sometimes with small amounts of shredded sagebrush bark mixed in. Although both kinds of bark are almost universally available, the juniper is definitely strongly preferred. No reason for this was evident to my eye and touch. In southeastern Colorado yucca fiber and shredded bark of the one-seed juniper are commonly used, either or both, as available. When both plants are used, yucca fiber sometimes forms an inner lining of the nest. Materials infrequently used in slight amounts are fine dry grass, soft feathers, seed hairs of milkweed and other plants, paper, and cotton threads.

One of the largest houses studied of the white-throated wood rat was on the raised center of the alluvial valley floor of John Brown Creek a mile southwest of Gateway, 4600 feet elevation. An old adult female, *N. a. brevicauda* (490624-1) was trapped at this house on 24 June 1949. The substrate was reddish, sandy and stony alluvial soil strewn with boulders. The house was erected in the space among several boulders lying close together and beside a large sage bush. (See Pl. 33, Fig. 1.) The habitats on the creek bottom and surrounding terrain are described on page 449.

The house was a low, substantially built dome composed of dry cow and horse dung (about 40 per cent), sage and juniper sticks (40 per cent), cactus debris (10 per cent), and a few wood chips and bones. The biggest stick used was 1¾ inches in greatest diameter and the longest was a slender branch 35 inches long. The height of the house was 24 inches on the upper side of the slope and 33 inches on the lower side. There were five entrances to the den, all on the ground level and leading under an overhanging boulder or post, as shown on the ground plan of the den in Figure 7. Outside of each entrance lay a large midden composed mostly of rat pellets and cactus spines. Another midden covered the ground under a projecting boulder at the southwest end of the house. Three smaller middens formed the floors of chambers inside the house.

A large central chamber containing a nest and food materials was above ground in the center of the dome, which formed a roof six inches thick. Nest A of three nests was at the southwest end of the central chamber. Dry and partly eaten pieces of prickly pear cactus were in front of the nest, filling part of the chamber to the roof. A consolidated fecal deposit 3½ inches thick was embedded in the floor beside the nest. Nest B was in the east corner of the large central chamber but at a slightly lower level than nest A. There was a supply of dry cactus joints beside nest B and a small consolidated midden, just as by nest A. From nest B a passage lead to a lower level and under the stem of a dead sage bush to a chamber in which nest C was situated directly below nest A. No food supply adjoined nest C. The outside dimensions of nest A were 9 by 7 inches. It was fully domed with a mouth 3 inches across and a pocket 4 inches deep. The material was entirely shredded juniper bark. All three nests had the same form and material. No underground burrow was found. Although the house was not fully dismantled to the ground, and a burrow could have been under one of the large boulders, the scarcity of soil in the middens supports the conclusion that no burrow was present.

The house was subjected to heavy rain for approximately an hour during a violent thunderstorm the day before the house was dismantled. At the time of examination the roof was damp several inches through, but the floor of the main central chamber was dry. The inside of nest A seemed slightly damp to the touch.

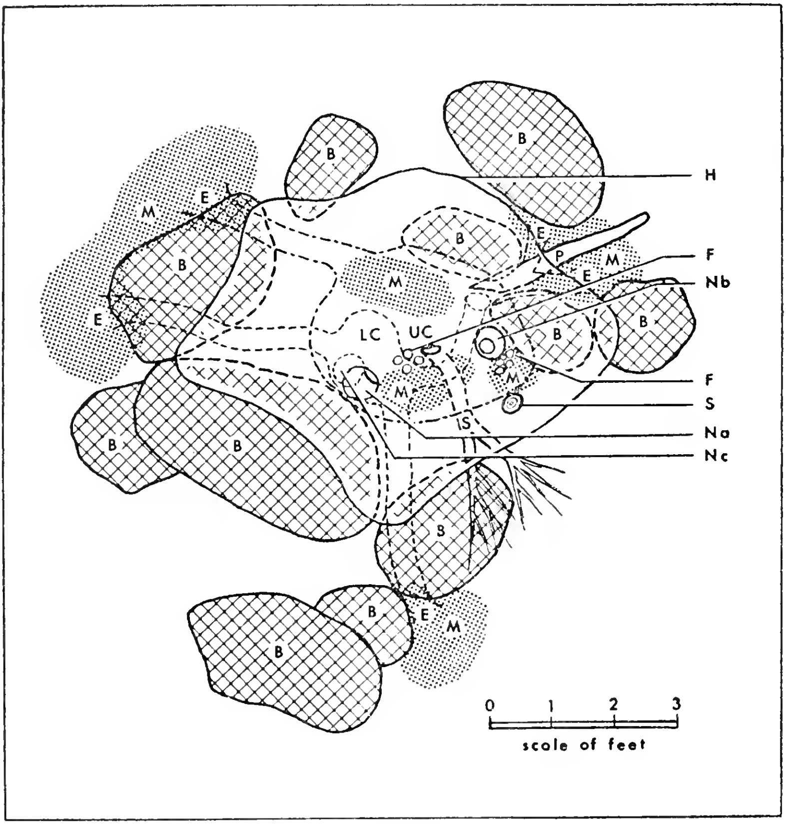


FIG. 7. Ground plan of house of *N. albigula* (490624-1) one mile southwest of Gateway. Legend: B, boulder; E, entrance; F, food; H, outline of house; LC, lower chamber; M, midden; Na, nest A; Nb, nest B; Nc, nest C; P, post; S, sagebrush stem; UC, upper chamber.

A large clump of skunkbush growing on the rocky creek bank sheltered a house with chambers and terraces at three levels on the bank. An adult male (490619-2) was trapped there on 19 June 1949. The house was built around and among numerous vigorous shoots and branches of skunkbush and the roots that had been exposed by creek erosion. The house was built of sage and juniper sticks, stock dung, and cactus debris. It was 52 inches long, 38 inches wide, 11 inches high at the top of the bank, and 21 inches high above the base of the house on the bank slope.

A single entrance to the house was on the upper side away from the creek, and at least three entrances were on the lower side by the creek. Four or more middens, none large, were on the bank below the house or on exposed root masses projecting from the bank. The entrance at the top of the bank led into a main chamber 15 inches high with the floor flush with the top of the bank. There were smaller chambers, passages, and lookout terraces on two lower levels along the bank and leading back into the bank among roots where I did not fully excavate. Since no nest was found it is presumed there was one underground.

A rock den of *N. albigula* was unusual in that the cleft occupied was vertical and had four den levels up to a height of seven feet above the base of the cliff. The sheltering cleft was an erosional crevice separating a pillar of rock from the low cliff of Shinarump conglomerate at the north edge of the creek valley bottom. The den looked old and in good condition, with a fair quantity of accumulated material. The latter consisted mostly of sage sticks, the most available kind on the valley bottom. There was also a large amount of prickly pear joints and spines, some stock dung, a deer bone, and three hanks of hair from remnants of a deer carcass at the base of the cliff 85 feet east of the den. Several old deposits of fecal and midden materials above ground level in the cleft were as much as six inches deep. Although the shelter resembled that selected by *N. cinerea*, the den was easily recognized as that of *N. albigula* by the profusion of cactus spines.

A den probably belonging to this species was examined four miles northwest of Gateway on 23 June 1949. Although no rat was caught and the den seemed in disuse, it contained such a large amount of cactus spines that it is hardly conceivable that *N. mexicana* or *N. cinerea* could have built it. The den was under one end of a large boulder where a piece had dropped away leaving a cleft. A Utah juniper standing beside the boulder sheltered the cleft and a small house 15 inches high between the cleft and the base of the juniper. Materials of the house were about equal parts stock dung, sticks, and dry cactus debris. The vertical crevice was nearly filled with the same materials, some of which were scattered also on top of the small lower block. Nearly all the cactus debris was of the most commonly occurring species, *Opuntia rhodantha*, but a small proportion of the spine areoles seemed to be of the more scarce species *O. phaeacantha*.

The little house adjoining the crevice contained a single chamber approximately five inches in diameter with a compact roof. From the chamber a passage led outside of the house under the juniper. Another passage led from the house chamber into the base of the crevice where it widened to form a chamber containing a nest partly embedded in the floor. The nest was made of shredded juniper bark and was semidomed (higher than cup-shaped, but not fully roofed).

This den is an interesting composite of a rock den and stick house in the early stage of formation. If it were reoccupied for a prolonged period the house would probably be built up higher than the top of the small rock and fill the space between the cleft and the juniper trunk. Such a composite den, with a house two feet high providing the main living space, was examined at the same locality. This den included, in addition, the hollow trunk of the juniper as a part of the living space.

A rock den typical of the numerous ones examined in horizontal clefts under projecting rock outcrops is that of an adult *N. a. laplataensis* trapped and released alive 5 miles east and 15 miles south of Mancos at 6500 feet elevation. This den (491117-1) was on the east rim of the valley of Cherry Creek. The habitat is described on page 451. The irregular weathering of the sandstone ledges resulted in a long low rock crevice two to three feet above the ground and a space between the lowest ledge and the ground. The crevice above the shelf measured 27 feet along the face of the outcrop, more than 6 feet deep, and 6 to 12 inches high at the front.

A large but not deep midden of cactus spines and rat pellets covered a considerable area of the shelf. Layers of midden in the back recesses of the crevice were cemented together in solid masses. Materials scattered on the midden included sticks of sagebrush and piñon, dry piñon cones, bark of piñon and juniper, pieces of horse dung, and a skull of a rock squirrel. A nest recovered from the rear of the crevice was composed of sagebrush bark (more than 90 per cent) and juniper bark (less than 10 per cent). More than a dozen green joints of prickly pear scattered far back in the crevice probably served as a temporary food store. At the north end of the shelf there was a bed of split juniper berries, probably the work of chipmunks (see section on food, p. 467).

A den entirely under a fallen boulder and having no adjoining house was studied two miles northeast of Bondad in the Florida Valley. A young adult male (491024-8) was caught at this den on 24 October 1949. The habitats there and at Bondad are described under *N. mexicana* (see p. 412). The boulder was 8 feet long, 6 feet wide, and 6 feet high. A piñon tree stood at the uphill end of the boulder and screened it with branches. The under surface of the rock sloped upward off the ground at the upper end so that there was a projecting overhang. The wood rat improved this sheltered space under the overhang by accumulating a pile of sticks and stock dung to wall off part of the space against the underside of the rock. Some of the sticks were as much as 2 feet long and 1½ inches thick. Slabs of piñon bark up to 12 inches in length, piñon cones, and dry joints of prickly pear *(Opuntia rhodantha)* were also accumulated among the sticks.

Removal of the accumulated materials at the upper end of the rock revealed a considerable space accessible to the rat, either as natural space or as excavated trenches. That this living space extended the full length of the boulder was indicated by a small amount of midden and sticks protruding from under the lower end of the boulder. Under the overhanging rock and accumulated sticks at the upper northeast corner there was a ball-shaped nest of shredded juniper bark lined with some unidentified fluffy material, perhaps some seed fiber. Food litter consisted mainly of juniper cuttings and *Opuntia* areoles. Only a few piñon needles were present as food litter. Approximately a gallon of juniper cuttings were stored inside an entrance under the northwest side of the boulder. Under sticks at the north end there were 34 green joints of *O. rhodantha,* 20 of which were piled in one hollow. A bed of bare juniper nutlets amounting to more than a pint in the northwest entrance was probably food litter dropped after the succulent husks had been stripped off by the rat.

A den (490819-2) one mile north of Cahone examined on 19 August 1949 was under a block of Dakota sandstone resting on a moderate rocky slope with southwestern exposure. The den was similar to the den northeast of Bondad but was under a much larger block, exceeding 20 feet in length, and sheltered a den of *N. mexicana* (490802-4) under the west end and one of *albigula* under the southeast side. Piñons and Utah junipers were numerous among the rocks. The common shrubs were sagebrush, rabbitbrush, squaw-apple, and antelope brush. There was a wide midden of cactus areoles *(O. polyacantha)*, rat pellets, and needles of piñon and juniper under a low cave-like, overhanging rim of the block. The midden was 3 feet long and 3 to 4 inches deep over most of its area but heaped up to a depth of 14 inches in the center. Mixed with the cactus spines were numerous sticks, pieces of cattle dung, and bones, as well as several Pueblo potsherds and a few stones. Although there was no fresh food litter on the midden, the mass of cactus spines far exceeded any seen at dens of *N. cinerea, mexicana*, or *lepida* in western Colorado. This den was the only indirect evidence found of the occurrence of *albigula* in an area where intergradation between *brevicauda* and *laplataensis* was to be expected.

Large houses in clumps of tree cactus one mile northwest of Higbee provided formidable protection for white-throated wood rats. The topography and vegetation there are described in the section on habitat (p. 451). A fine den was dismantled in an unusually dense clump of tree cactus at which two *N. a. warreni* had been captured (500516-5♂ and 500516-6♀ pregnant) on 16 May 1950. The drainage at the site was unfavorable because the bottom of the house was only two feet higher than the bottom of a small wash and ten feet away horizontally. The clump of tree cactus was 7 feet high, 10 feet long, and 9 feet wide. The house was 23 inches high, 63 inches long, and 55 inches wide. Joints, sticks, and areoles of the tree cactus made up more than 90 per cent of the bulk of the house materials. The remainder was livestock dung and a few small stones. Tree cactus was estimated to compose more than 99 per cent of the food litter, in the form of gnawed joints, fruits, and areoles.

There were four entrances to the house located on the northeast, east, southeast, and southwest sides. The last-mentioned entrance was plugged with cactus litter. No entrance was present on the west side which abutted against the main stem of the tree cactus. Middens containing rat pellets, cactus spines, and some soil were piled outside three of the entrances. A heap of tree cactus joints had been piled onto dead drooping limbs of the tree cactus to form the "roof" of the house. There was a large main living chamber on the ground level under the northwest side of the house next to the main stem of the cactus. The southwest side of the house was closed off into several small chambers and passages most of which were stuffed with joints of tree cactus or masses of spines. A dome-shaped nest was on the soil surface on the southwest side of the main chamber. Materials of the nest were more than 95 per cent yucca fibers, with a few feathers, fine dry forbs and grass blades. The nest was small, only 7½ and 6 inches in length and breadth, 5½ inches high, and with inside dimensions of 4 by 4 inches and 3 inches high.

Although the house was cleared to the ground level, no underground burrow was found. The soil was dry and hard, a light brown sandy loam. Perhaps the large amount of sheltered living space above ground made the excavation of underground passages unnecessary.

The floor of the main chamber was covered with a bed of tree cactus areoles 1 to 1½ inches deep with fruit debris intermixed. Although it is conceivable that a layer of cactus spines at the entrance to a den might be prepared primarily for defense, this bed of spines in the heart of the house could have had no such protective value and must have been formed solely as a by-product of feeding.

A somewhat smaller house at the same locality was in a tree cactus providing much less shelter, the cactus growing only 4½ feet high. The house measured 20 inches high, 54 inches long, and 50 inches wide. A considerable part of the living space of the den was below the ground level. The soil and middens were similar to those at the previous den. The house was built almost entirely of tree cactus debris with a few pieces of stock dung and dry weed stalks. A bare runway encircled the house against its base and on the ground. The body of the house was a hollow dome covering a large central chamber having, as a floor, a midden resting on the low basal branches of the tree cactus. Below these branches and around the underground stem there was a larger ring chamber entrenched 2 to 3 inches in the soil. There was no lengthy passage inside the house or underground but a short burrow led from the side of the ring chamber down to a blind chamber barely below ground. A nest of mixed yucca fibers and fine grass was on the north side of the entrenched ring chamber with its mouth facing the stem of the cactus. The nest was almost roofed over. The occupant of this house was an adult male (500516-9).

A house of simpler plan in the midst of a skunkbush thicket was composed mostly of livestock dung with some sticks and twigs of skunkbush, sticks of tree cactus and juniper, and weed stalks. The house was 17 inches high, 51 inches long, and 47 inches wide. Its low outline and much detritus from the thicket made it look old and in run-down condition, but it was occupied by an adult male (500516-13). There were only two entrances, a large one at the west end and a smaller one at the east end. There was a large midden of fecal pellets and soil outside of each entrance. The midden at the west end was heaped up above the ground like a ramp. The low broad roof, anchored and supported by *Rhus* stems and branches, covered a large central chamber, the floor of which was sunk below the nearly prostrate branches and between roots. Earth had been excavated from under the house and dumped on the middens, enlarging the central chamber to a depth of 3 to 6 inches below the ground surface. The chamber was 40 inches long, and 14 inches deep near the center of the house. The roof was from 4 to 7 inches thick. A nest below ground on the south side of the chamber was a hollow ball of yucca fibers and juniper bark in about equal proportions, with most of the yucca inside and the juniper bark outside. No lower chamber or burrow was found, but the soil was not fully cleared of all house debris.

At a large den of *N. a. warreni* situated between two boulders in a low thicket of skunkbush on the lower slope of Two Buttes peak, 4500 feet elevation, an adult male (500509-6) and a pregnant female (500509-7) were trapped on 9 May 1950. The habitats in the vicinity of Two Buttes are described on page 452. The den consisted of a broad heap of accumulated materials between the two principal boulders, supplemented by low spaces under the buolders. Numerous stems and branches of skunkbush anchored and shielded the house.

The house was 66 inches long, 45 inches wide, 22 inches high on the lower side of the slope, and flush with the slope on the upper side. The largest boulder was 3½ feet high. Volumetrically the roof was 40 per cent red sandstone (small pieces), 40 per cent dry stalks and small sticks, and 20 per cent rabbit bones and cattle dung. Of the four entrances, two were downhill, one on each side of the largest boulder, one was uphill between stones at the side of the house, and one was near the top of the house. The main midden was on the slope below the lowest downhill entrance, and there was a small midden outside the upper side-entrance. Passages within the house were on two levels. A nest chamber on the lower level rested on the soil between the two main boulders. The single nest, nearly but not completely roofed over, was 11 inches long, 8 inches wide from mouth to rear, 8 inches high, and 4½ inches deep inside. The mouth was 4½ inches wide and 3 inches high. The nest was almost entirely fibers of *Yucca glauca,* with bits and shreds of paper and cardboard gnawed from larger pieces brought into the den. There was a little more than a quart of pieces of yucca blades and three fruits in the nest chamber and under the edge of one of the rocks. The *Rhus* thicket and yucca plants near the den had been moderately pruned. Cuttings of yucca lay in the lower entrance. Although I excavated some of the soil underneath the house, I found no escape tunnel. Because of the absence of cactus in the vicinity there was no bed of cactus spines at this den.

A den underneath and behind small talus boulders, higher up the slope from the above-mentioned house, contained much litter accumulated about the crevices and entrances, but there was no structure that could be termed a house. The bulk of the materials consisted of small weed stalks and dry twigs, presumably gathered on the ground. Other den materials were dry yucca stalks and stem bases, cow dung, small bones and assorted odds and ends of human origin. The largest boulder covering the den was 5 feet by 3 feet by 2 feet high, and sheltered a nest of shredded yucca fibers and paper.

On the slope of a tributary valley leading into Two Buttes Creek, a large house (500509-14) at the base of a one-seed juniper was dismantled. The site was a moderate upper slope with thin stony soil and excellent drainage. The house, shown in Pl. 32, Fig. 1, was built up through the basal branches, which were widely spreading at the ground level. The dense healthy condition of the juniper provided much cover close to the ground on all sides. The greatest bulk of the den materials consisted of small sticks and twigs of juniper mixed with dry weed stalks. About 25 per cent of the material was cow dung and about 20 per cent was small pieces of reddish sandstone. Insignificant amounts of other materials were dry yucca blades and stem fragments, bones, and *Buteo* feathers. Cuttings of juniper foliage provided most of the food litter, and yucca blades a lesser amount. Since there was no live cactus within 100 feet of the den, it was not surprising that there was no bed of cactus spines. A few areoles of *Opuntia humifusa* nevertheless were present.

The stick house, dome-shaped with its summit on the uphill side of the main central stems of the tree, was 32 inches high on the uphill side and 14 inches on the downhill side. Diameters were 40 and 38 inches. Five entrances, all slightly above ground, led into the house on the east (downhill), south, and west sides. Broad coalescing middens of rat pellets, juniper needles, and soil lay outside of three of the entrances, forming an apron skirting the downhill side of the house. Bare runways on the ground along the base of the tree on the lower side were partly overhung by projecting basal branches of the tree. The dome of the house supported one feeding chamber on a level with the ground uphill. On the south side a long chamber or passage ran under a long prostrate limb at a level lower than the feeding chamber. The west end of this chamber was on the sloping soil and the east end on a bed of food litter. A domed nest composed entirely of yucca fibers was embedded in the soil under the prostrate limb (see Pl. 34, Fig. 1.) Additional passages on the ground extended down and around the juniper, under limbs and sheltering house-materials. Search for an underground tunnel revealed none. Basically this house was a central chamber with a lower ring, as was typical of houses in tree cactus, but in this den the ring was irregularly broken by basal limbs of juniper and the sloping hillside.

A noteworthy house (500509-15) was in a juniper on the lower slope near the bottom of the valley. The tree grew in the middle of a shallow rock wash where runoff from the side of the valley had been concentrated in a shallow channel and had swept the underlying bedrock bare of soil and mantle rock. (See Pl. 35, Fig. 1.) The base of the house stood only a few inches higher than the floor of the rock channel. It was difficult to see how the occupant of this house could avoid being flooded out by any substantial downpour such as might accompany a heavy thunderstorm. Nevertheless, this house was one of the most massive and substantial that I have seen in Colorado and seemed to have been occupied by more than one generation of rats. The house was solidly roofed, almost shingled, with flat pieces of red sandstone and of dry cow dung, together comprising an estimated 50 per cent of the mass of the house materials. Weed stalks, juniper detritus (but not large sticks) and fragments of yucca made up the balance of the house, which was 16 inches high on the upstream, north side and 26 inches on the downstream side. The length, parallel to the wash, was 58 inches and the width, 51 inches.

Four entrances seemed to be in use, one near the top of the house on the west side, two converging on a single Y-shaped hallway at the southwest side, at ground level, and one on the east side at ground level. Indistinct middens of rat pellets and juniper litter fringed the southwest and east sides of the house. The middens contained no appreciable amount of soil. In addition to the west entrance, which opened out beneath a limb where house debris did not easily lodge, there were three other smaller openings in similar situations. These seemed not to be in use as entrances and could perhaps be referred to as "windows." On the west side near the ground level a low terrace overlooked that half of the wash. The dome of the house covered a main central living chamber 13 inches high and 26 inches in diameter. The roof, six inches thick, was supported by arching lower limbs of the juniper. The chamber was floored with fresh food litter, about 80 per cent of which consisted of juniper twigs, needles, and cuttings. Small lateral chambers were divided off from the main chamber by basal juniper branches. A curving passage led from the upper west entrance down into the main central chamber.

A ball-shaped nest of yucca fibers, facing north, was imbedded in litter on the floor of the south side of the main chamber. There was no underground passage or escape tunnel.

Because of solid construction and anchorage, and the absence of an entrance on the uphill side, this house could withstand and deflect a considerable rush of water without damage. There were no underground spaces in which the rat could be trapped. If the water rose enough to cover the floor of the main chamber, the occupant could easily climb into the top of the house, or even into the juniper tree.

A den with extensive burrows was under a clump of yucca on the plains upland between Two Buttes peak and Two Buttes Creek. An adult female (500511-1) was trapped there on 11 May 1949. A low mound of dry cow dung in the midst of the yucca might be called a house, but all the living chambers were below ground. An open patch of yucca 35 feet long and 15 feet wide (paced) grew on an elongate mound of soft earth 1 to 2½ feet higher than the surrounding ground. Most of the yuccas were partly yellow, probably caused by extensive exposure and damage of roots from the burrows of the wood rat and of kangaroo rats penetrating the mound.

The house or heap of material measured 16 inches high on the lower side of the slope, 7 inches high on the upper side, 50 inches long, and 24 inches wide. It was a solid mass of approximately 75 per cent cow dung; 15 to 20 per cent dry sunflower stalks; and a few weed stalks, yucca stalks and dry yucca blades. There was a large chamber under the house and sunk in the soil below the dead lower leaves of yucca lying flush with the ground surface. Entrances on four sides of the house led down to the central chamber, in which there was much food litter, mostly cut leaves of yucca. Middens at two of the entrances, consisted mostly of loose earth with some rat pellets mixed in. Cut pieces of yucca blades lay scattered on the middens.

From the main central chamber a winding burrow extended under the thicket. This main burrow was excavated only for a distance of eight feet. It averaged 12 to 14 inches in depth below the surface and 3 to 3½ inches in diameter. The soil was a light brown sandy loam, slightly damp below a depth of six inches. Several side tunnels branched off to entrances under dense cover of yuccas. A network of surface runways traversed the mound of earth, mostly under cover of yuccas. A nest of yucca fibers was in a blind chamber off the main tunnel seven feet east of the house. The chamber contained also food litter.

At a den in the hollow trunk of a plains cottonwood tree an adult male (500520-2) was trapped one mile northwest of Higbee on 20 May 1954. The tree originally had a main fork close to the ground, but half of the tree had fallen leaving only the more erect fork standing with a rotten hollow trunk. The tree stood on the bank of a small creek and was surrounded by one-seed junipers. There was almost no material accumulated about the base of the tree, only a few dead cottonwood twigs, small sticks, bark and rotten wood, a few pieces of cow dung, and an owl pellet. The base of the hollow trunk was filled a foot deep with food litter consisting mostly of areoles and a few joints of tree cactus with some juniper cuttings and lesser items. A large ball-shaped nest in the hollow trunk two feet above the ground was composed of shredded juniper bark outside and yucca fibers inside. Only two small clumps of *Yucca* *glauca* were growing within 100 feet of the den. Nine fresh joints of tree cactus were in the space close around the nest.

FOOD

The succulent joints of various species of cacti are the dominant kind of food eaten by the white-throated wood rat. Wherever this species of rat is living, one species of cactus or another is usually the most important single item in its diet. Juniper needles are next in importance as food. *Yucca* blades and leaves of various shrubs and forbs are also commonly eaten, but in less quantity than cactus and juniper. Grasses are sometimes eaten in small amounts that are inconsequential in comparison with the amounts of cactus eaten.

The remains of cactus left in the food litter consist mostly of spine-areoles left after the eating away of all the succulent flesh of the joints. The spines are commonly so abundant as to form a dense layer or enmeshed mass intermingled with fecal pellets. Among the spines, or more usually on the surface of the spiny midden, there may be numerous detached green joints and partly eaten pieces of joints. Spiny cactus fruits may also be present and partly eaten.

It is not always possible to distinguish the cactus joints that were brought into the den for food from the joints that were brought in to add to the shelter material of the den. The latter material is generally dry and ungnawed, possibly picked up as dead dry joints originally, but sometimes cut when green and added to the pile. Since the wood rat sometimes feeds on pieces of cactus that have been added to the den structure, it is evident that the rat can utilize such material for a time as shelter and then as food. Vorhies and Taylor (1940: 505) have described such dual use of mesquite beans, as well as cholla cactus, by *N. albigula albigula.*

A further change in the use of cactus takes place after joints which have been part of the den structure are eaten. As the succulent pulp is consumed the areoles are dropped and accumulate as a spiny bed of food litter. This accumulation of spines in the entranceways and along some of the paths radiating away from the house then serves to protect the den against entry by mammalian predators. Thus cactus which was first used as shelter, becomes a source of food, and finally a different kind of protection. Hamilton (1939: 282) has said that these rats "pave their runways with the needle-sharp spine clusters" as a method of defense. Hill (1942: 213) has described such dens in a stand of *Opuntia fulgida* in Arizona. There seems to be little doubt of the defensive value of such a bed of spines, covering a route of access to the house, but the actions of the rat are probably not primarily a deliberate building of defenses but a haphazard discarding of inedible food refuse. Such an interpretation of behavior is born out by the examination of the house of *N. a. warreni* (500516-5), in which the floor of the main living chamber in the center of the house was "paved" with a bed 1 to 1½ inches deep of tree cactus areoles and fruit debris. Such a layer of spines in the very heart of the house could have little value for defense.

The fruits, flowers, stems, and woody parts of plants are not ordinarily staple items of the diet, though they may be important at certain seasons. The only fruits found frequently as food at the dens studied in Colorado were those of cactus and juniper. Shells of piñon seeds and acorn shells were sometimes present, but neither unopened piñon seeds nor acorns were found. Fruits of cholla and prickly pear cacti were nearly always found among more numerous vegetative joints of the same species, not as separate accumulations.

Juniper berries were usually scattered among the larger amounts of foliage cuttings of juniper, or less frequently spread over a separate part of the den floor or rock shelf. Only the pulpy husks of the berries seemed usually to be eaten, leaving the bony nutlets unopened. An example of this was at den 491024-8, where there was a bed of bare, uncracked juniper nutlets, amounting to more than a pint, in one entrance under the sheltering boulder.

Occasionally juniper berries, which had been split open through the husk and seed, were left in and about the den, sometimes on exposed rocks. Also some nutlets which had been split open, and from which husks and kernels had been removed, were left in and about the den. For instance, a bed of split juniper berries was on a ledge at one end of den 491117-1. But the splitting open of juniper berries and nutlets seems to be the work of squirrels or chipmunks. Possibly these or other rodents are attracted to wood rat dens by the berries and numerous husked nutlets left by the rats. Whether wood rats themselves crack open the seeds and eat the kernels, as claimed by Bailey (1931: 179) for *N. a. albigula,* could be conclusively settled by nocturnal observation of a favorably situated den with the aid of a red light.

Shells of piñon seeds were found not uncommonly in the food litter of *N. albigula,* but never in concentrated accumulations. They sometimes occurred with foliage cuttings of piñon and sometimes with no other piñon debris. The needles of piñon are not very much liked. Of the plants more important to the white-throated wood rat, the piñon seems to be one of the few of which the fruit is more highly regarded as food than is the foliage.

The species of *Artemisia* are but little used for food, even when abundant close to the den. *Gutierrezia*, likewise, is little used and seems to be disliked, although it is also an abundant plant throughout much of the range of *N. albigula* in Colorado.

Nearly all the food plants of *N. albigula* are abundant xerophytic plants of the Upper Sonoran Life-zone. Mesophytic plants growing near water, and plants more characteristic of the Transition Life-zone are less commonly found close to the dens of this rat and are seldom eaten when they are available. There are a few differences in food habits between the rats living west of the Continental Divide and those of the High Plains Region. The latter are much less partial to the prickly pear cacti, probably because of the abundance there of a superior species of *Opuntia*, the tree cactus, which is the prime choice for food wherever it is within reach. Where it is not found and the prickly pears are scarce, *Yucca* is of greater importance and is collected in larger quantities.

The only pronounced difference in food preference that has no apparent relation to geography, habitat, or availability is the high preference for skunkbush by *N. a. warreni* in the High Plains Region —9 times available and 7 times eaten. Skunkbush stands at the very bottom of the list for both subspecies west of the Continental Divide—6 times available and never eaten by *brevicauda*, and 11 times available and never eaten by *laplataensis*. If this is an inherent difference in the tastes of these rats, its adaptive significance, if any, is unknown.

A less distinct difference may exist in preference for saltbush, which stands high on the list of plants eaten by the two western subspecies. Saltbush was available within 100 feet of only two dens of *N. a. warreni* and was not eaten by the rats at either den.

The food habits of *N. albigula* are rather highly specialized for subsistence on the succulent flesh of cactus in arid and semiarid regions of the Southwest. Many other plants, especially juniper, are also eaten, and may take the place of cactus locally where cactus is absent, but the geographic range of *N. albigula* does not extend outside of areas in which some species of cactus is generally abundant. This specialization of *N. albigula* is similar to that of *N. micropus*, which also prefers cactus, and is in contrast to the more generalized food habits of *N. mexicana* and *N. cinerea*.

In the present study the data obtained on food can best be presented separately for each subspecies of the white-throated wood rat, because of differences in the plants available in different parts of its range. Such treatment also facilitates comparison with sympatric species of wood rats.

N. albigula brevicauda

Some preferred foods of *brevicauda* (from a study of only seven dens) are prickly pears (*Opuntia phaecantha* and *O. polyacantha*), Utah juniper, saltbush, and yucca. Skunkbush, sagebrush, and cottonwood leaves seem to be rarely eaten even when easily available.

Information concerning food is presented in the following paragraphs for each of the dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

One Mile Southwest of Gateway, 4600 Feet

19 June 1949.—490619-1. + *Opuntia polyacantha,* + *Opuntia phaeacantha,* * *Juniperus utahensis,* * *Atriplex canescens,* -- *Coleogyne ramosissima,* -- *Artemisia tridentata,* -- *Yucca baccata; Pinus edulis, Fraxinus anomala, Rhus trilobata, Polanisia trachysperma.*

490619-2. + *Opuntia phaeacantha,* + *O. polyacantha,* * *Salsola kali; Juniperus utahensis, Pinus edulis, Rhus trilobata, Artemisia tridentata, Atriplex canescens, Chrysothamnus, Chrysopsis.* Nearly all of the food litter consisted of cactus areoles, pieces of joints, and fruits of the two species of *Opuntia.* A single clump of the pincushion cactus *(Echinocereus coccineus)* was growing 110± feet from the den, but no spines of this species were found in the midden.

490619-3. * *Opuntia phacacantha,* * *O. polyacantha,* * *Juniperus utahensis,* - *Atriplex canescens,* - *Salsola kali; Populus wislizeni, Artemisia tridentata, Rhus trilobata, Melilotus, Echinocereus coccineus.* Sweet clover growing by the den and by the creek 30 feet away had been pruned. The pincushion cactus grew approximately 100 feet from the den.

490619-6. + *Hilaria jamesii,* * *Juniperus utahensis,* * *Coleogyne ramosissima,* * *Opuntia phaeacantha; Artemisia tridentata, Rhus trilobata, Yucca baccata, Ephedra viridis.* None of the food litter was fresh. There were many dry basal clumps of partly eaten *Hilaria.* This den was small and looked more like the work of *N. mexicana.* Perhaps the *N. albigula* caught here was a visitor from a large den 125 feet away that had a good midden of cactus spines.

490619-7. + *Opuntia polyacantha,* + *Opuntia phaeacantha,* * *Atriplex canescens,* - *Lupinus,* - *Juniperus utahensis,* -- *Yucca angustissima; Populus wislizeni, Artemisia tridentata, Rhus trilobata.* Remains of the lupine were a few dry pods in the midden. One gnawed seed capsule of the *Yucca* was among the food litter, but no *Yucca* was growing within 100 feet of the den.

24 June 1949.—490624-1. + *Opuntia polyacantha,* + *O. phaeacantha,* - *Echinocereus coccineus,* - *Juniperus utahensis; Pinus edulis, Populus wislizeni, Artemisia tridentata, Rhus trilobata, Fendlera rupicola, Sphaeralcea parvifolia, Stanleya pinnata.* A single cottonwood grew 100 feet away from the den.

One Mile Northeast of Naturita, 5900 Feet

26 June 1949.—490626-2. + *Opuntia polyacantha,* * *Juniperus utahensis,* * *Pinus edulis,* * *Hilaria jamesii,* * *Atriplex canescens,* - *Yucca baccata,* - *Mirabilis multiflora; Artemisia tridentata, Yucca angustissima?, Stanleya pinnata pinnata.* A few pieces of *Yucca baccata* leaves 1 to 2 inches long were in the den, but no plants were growing within 100 feet of the den. Considerable *Hilaria* grass stalks had been clipped off close to the ground.

A summary of data on food obtained at seven dens of *N. a. brevicauda* is presented in Table 25 in order to show the relative preference for each kind of food plant. High preference is indicated by high percentage of dens at which the available plant is eaten. The amounts of each plant in the food litter and the distances of the available plants from the dens were also considered in arranging the plants roughly in order of decreasing preference. Only a few kinds of plants occurred often enough to show significant differences in preferences.

TABLE 25.—PLANTS AVAILABLE AND USED AS FOOD AT 7 DENS OF N. A. BREVICAUDA (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Opuntia phaeacantha	6	6	1
Opuntia polyacantha	6	6	1
Juniperus utahensis	7	6	
Atriplex canescens	5	4	
Yucca	3	3	
Coleogyne ramosissima	2	2	
Salsola kali	2	2	
Hilaria jamesii	2	2	
Lupinus	1	1	
Mirabilis multiflora	1	1	
Echinocereus coccineus	2	1	
Pinus edulis	4	1	
Artemisia tridentata	7	1	
Sphaeralcea parvifolia	1		
Chrysopsis	1		
Polanisia trachysperma	1		
Ephedra viridis	1		
Chrysothamnus	1		
Fendlera rupicola	1		
Fraxinus anomala	1		
Melilotus	1		
Stanleya pinnata	1		
Populus wislizeni	3		
Rhus trilobata	6		

N. albigula laplataensis

Among the most preferred food plants of _laplataensis_ are prickly pears, Utah juniper, rat-tail cactus, _Echinocereus coccineus, Echinocactus whipplei,_ scrub oak, winterfat, _Atriplex,_ and matrimony vine. The leaves of the last three plants are eaten, as well as the leaves and acorns of the scrub oak.

The following plants seem to be but little used as food by _laplataensis,_ even when easily available close to the den: skunkbush, mountain-mahogany, antelope brush, cottonwood, snakewood, serviceberry, rabbitbrush, and the sages (_Artemisia_).

Information concerning food is presented in the following paragraphs for each of 13 dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Bondad, 6050 Feet

15 June 1949.—490615-3. + _Opuntia rhodantha,_ * _Artemisia tridentata,_ -- _Chrysopsis villosa,_ -- _Melilotus; Juniperus scopulorum, Populus angustifolia, Rhus trilobata, Cercocarpus montanus, Yucca baccata._ Cactus spines were abundant in the midden, and there were two fresh green joints uneaten on the chamber floor just inside the main entrance. A nearly dead clump of skunkbush had been slightly pruned.

One Mile North of Cahone, 6900 Feet

19 August 1949.—490819-2. + _Opuntia polyacantha,_ * _Juniperus utahensis,_ * _Pinus edulis,_ - _Chrysopsis; Artemisia tridentata, Chrysothamnus nauseosus, Peraphyllum ramosissimum, Purshia tridentata, Gutierrezia, Rhus trilobata._ A large midden of cactus spines, constituting perhaps 75 per cent of the food litter, could only have been accumulated at this locality by _N. albigula,_ not by the specimen of _N. mexicana inopinata_ that was trapped at this den. Numerous dens of the latter species at this locality contained no midden of cactus spines.

Five Miles East and Fifteen Miles South of Mancos, 6700 Feet

13 August 1949.—490813-1. + _Opuntia polyacantha,_ * _Echinocereus coccineus,_ * _Artemisia tridentata,_ * _Juniperus utahensis,_ * _Lycium pallidum,_ * _Pinus edulis,_ - _Echinocactus whipplei,_ - _Salsola kali._ Foliage cuttings of the sagebrush and juniper were present but none of piñon, only shells of piñon nuts.

27 August 1949.—490827-1. + _Opuntia davisii,_ + _Eurotia lanata,_ + _Quercus gambellii,_ * _Artemisia tridentata,_ * _Atriplex canescens,_ * _Juniperus utahensis,_ * _Opuntia polyacantha,_ * _O. hystricina,_ * _Bromus tectorum,_ * _Smilacina_ sp., * _Penstemon,_ * _Sphaeralcea,_ * _Hymenoxys richardsonii,_ - _Echinocereus coccineus,_ -- _Echinocactus whipplei,_ -- _Atriplex_ cf. _A. nuttallii,_ -- _Salsola kali; Pinus edulis, Juniperus scopulorum, Ephedra viridis, Gutierrezia, Acer negundo, Salix, Rhus trilobata, Rosa, Clematis ligusticifolia._ The greatest amount of any food item was of joints and pieces of rat-tail cactus. There was a lesser amount of loose areoles. All cactus seems to have formed not much more than one half of the diet of the resident of this den, if that much. Four or five gallons of rat-tail cactus, scrub oak, and winterfat were stored in a vertical crevice.

490827-2. + *Opuntia polyacantha*, + *Juniperus utahensis*, * *Atriplex canescens*, - *Pinus edulis*, -- *Quercus gambellii*, -- *Artemisia tridentata*, -- *Lycium pallidum*; *Populus angustifolia, Chrysothamnus nauseosus, Gutierrezia, Rhus trilobata, Artemisia frigida, Echinocereus coccineus, Salsola kali, Sphaeralcea* sp., *Hymenoxys richardsonii*.

17 November 1949.—491117-1. + *Opuntia rhodantha*, * *Juniperus utahensis*, * *Pinus edulis*, * *Artemisia tridentata*, * *Marrubium vulgare*, * *Bromus tectorum*, - *Echinocereus coccineus*, - *Hymenoxys richardsonii*, - *Quercus gambellii*, -- *Echinocactus whipplei*; *Chrysothamnus nauseosus, Rhus trilobata, Gutierrezia, Lycium pallidum, Salsola kali*. There were cuttings of seed heads of brome grass and flower stalks of *Hymenoxys*. A few acorn shells must have been brought from a scrub oak thicket 105 feet away and across a road from the rat den.

491117-2. + *Opuntia rhodantha*, * *Juniperus utahensis*, * *Echinocereus coccineus*, * *Echinocactus whipplei*, * *Pinus edulis*, * *Lycium pallidum*, * *Eurotia lanata*, - *Quercus gambellii*, -- *Chrysothamnus nauseosus*; *Artemisia tridentata, Rhus trilobata, Atriplex canescens, Salsola kali, Marrubium vulgare, Hymenoxys richardsonii*. *Lycium* growing by the den was pruned. Two heads of pincushion cactus had been gnawed out of a cluster growing on the wooded flat above the rimrock.

Two Miles South and Four Miles West of Cortez, 5900 Feet

12 September 1948.—480912-1. + *Opuntia davisii*, + *O. polyacantha*, * *Opuntia phaeacantha*, * *Amelanchier* sp., * *Chrysothamnus nauseosus*, * *Gutierrezia sarothrae microcephala*, * *Juniperus utahensis*, * *Salsola kali*, * *Echinocereus coccineus*, * *Mammillaria vivipara*, - *Echinocactus whipplei*, -- *Atriplex confertifolia*; *Pinus edulis, Rhus trilobata, Artemisia tridentata, Ambrosia trifida, Oryzopsis hymenoides, Hilaria jamesii, Sporobolus cryptandrus, Agropyron smithii*. Rabbitbrush near the den had been heavily pruned and serviceberry somewhat pruned.

Six Miles East and Seventeen Miles South of Cortez, 5600 Feet

15 September 1949.—490915-1. + *Opuntia polyacantha*, + *Juniperus utahensis*, * *Atriplex confertifolia*, * *Penstemon* sp., - *Echinocactus whipplei*, - *Echinocereus coccineus*; *Pinus edulis, Artemisia tridentata, Ephedra viridis, Amelanchier utahensis, Cercocarpus montanus, Chrysothamnus nauseosus, Forestiera neomexicana, Rhus trilobata, Gutierrezia*. Food litter of *Penstemon* consisted of stalks bearing seed capsules.

490915-4. + *Opuntia polyacantha*, + *Lycium pallidum*, * *Opuntia hystricina*, * *Atriplex confertifolia*, * *Echinocereus coccineus*, * *Ephedra viridis*, * *Juniperus utahensis*, * *Chenopodium incanum*, * *Euphorbia serpyllifolia?*, - *Astragalus racemosus*, - *Yucca baccata*, - *Elymus macounii*, -- *Lepidium* sp., -- *Pinus edulis*, -- *Tetradymia spinosa*, -- *Gutierrezia*, -- *Physalis* sp.; *Artemisia tridentata*. It is significant that the only plant observed growing within 100 feet of the den that was not utilized for food was sagebrush, the most abundant shrub in the area. Spines of the pincushion cactus must have come from plants growing more than 100 feet away from the den. Although cactus spines and *Lycium* twigs constituted the main bulk of the food litter, the number of plant species identified from the food litter exceeded the number of species observed growing within 100 feet of the den.

490915-5. + *Opuntia rhodantha*, + *Opuntia hystricina*, * *Atriplex confertifolia*, * *Sarcobatus vermiculatus*, * *Juniperus utahensis*, - *Yucca baccata*, -- *Echinocereus coccineus*, -- *Tetradymia spinosa; Pinus edulis, Artemisia tridentata, Gutierrezia*. A piñon tree screened the den entrance but was not used for food. No bush of *Tetradymia* was seen within 100 feet of the den, but a twig was found in the food litter.

Two Miles Northeast of Bondad, 6100 Feet

24 October 1949.—491024-1. + *Opuntia rhodantha*, + *Opuntia davisii*, * *Juniperus utahensis*, * *Artemisia tridentata*, * *Quercus gambellii*, * *Melilotus officinalis*, - *Mirabilis linearis*, - *Mirabilis multiflora*, -- *Xanthium*, -- *Physalis* sp.; *Juniperus scopulorum, Pinus edulis, Rhus trilobata, Amelanchier utahensis, Fendlera rupicola, Purshia tridentata, Chrysothamnus nauseosus, Gutierrezia, Artemisia ludoviciana, Chrysopsis, Eriogonum, Salsola kali, Sphaeralcea.*

491024-8. + *Opuntia rhodantha*, * *Juniperus utahensis*, * *Juniperus scopulorum*, * *Quercus gambellii*, - *Pinus edulis*, -- *Fendlera rupicola; Artemisia tridentata, Amelanchier utahensis, Rhus trilobata, Cercocarpus montanus, Purshia tridentata, Gutierrezia, Opuntia davisii, Hymenoxys richardsonii, Artemisia ludoviciana.* Green cactus joints and juniper foliage cuttings were stored in the den.

A summary of food data obtained at all 13 dens of *N. a. laplataensis* is presented in Table 26 in order to show the relative preference for each kind of food plant. High relative preference is indicated by high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants to the dens were also considered in arranging the plants roughly in order of decreasing preference.

It may be noted in Table 26 that prickly pears, Utah junipers, piñon, and sagebrush were available at nearly every den studied, and that the percentages of dens with these plants available at which each kind of plant was eaten were 100, 100, 58, and 46, respectively. But these figures do not reflect the quantities of each plant eaten, only with the occurrences in food litter. In order to show better the relative use of these four common plants, the amounts eaten may be roughly summarized by assigning numerical values to the symbols of abundance used with the plant names on pages 471 to 473, as follows: ++, 5; +, 4; *, 3; -, 2; --, 1; and absence of a symbol for an available plant, 0. The numerical values for each of the four food plants are totaled below for the 13 dens and divided by the numbers of availabilities to obtain an average value that may be called an *index of preference:*

	prickly pears	*juniper*	*piñon*	*sagebrush*
	4	3	3	3
	4	3	3	0
	4	3	0	3
	3&3 (2 species)	4	2	3
	4	3	3	1
	4	3	3	3
	4	3	0	0
	4&3 (2 species)	4	0	0
	4	3	1	0
	4&3 (2 species)	3	0	0
	4&4 (2 species)	3	0	0
	4	3	2	3
	4			0
	—	—	—	—
total	64	38	17	16
avail.	17	12	12	13
index of preference	3.76	3.17	1.42	1.23

The indices of preference indicate that the average amount of prickly pear eaten, per den at which it was available, is somewhat greater than that of juniper. They also indicate that the average amounts of piñon and sagebrush eaten are much less than of either juniper or prickly pear.

TABLE 26.—PLANTS AVAILABLE AND USED AS FOOD AT 13 DENS OF N. A. LAPLATAENSIS (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE).

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Opuntia (*Platyopuntia*, including 6 *rhodantha*, 7 *polyacantha*, 3 *hystricina*, and 1 *phaeacantha*)	17	17 (100%)	3
Juniperus utahensis	12	12 (100%)	3
Opuntia davisii	4	3 (75%)	2
Echinocereus coccineus	8	8 (100%)	....
Echinocactus whipplei	6	6 (100%)	....
Quercus gambellii	5	6 (120%)	1
Eurotia lanata	2	2 (100%)	1
Atriplex	8	7 (88%)	....
Lycium pallidum	5	4 (80%)	....
Pinus edulis	12	7 (58%)	....
Penstemon	2	2 (100%)	....
Mirabilis	2	2 (100%)	....

TABLE 26.—*Concluded*

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Tetradymia spinosa	2	2 (100%)	
Bromus tectorum	2	2 (100%)	
Melilotus	2	2 (100%)	
Physalis	2	2 (100%)	
Yucca baccata	3	2 (67%)	
Chrysopsis	3	2 (67%)	
Artemisia tridentata	13	6 (46%)	
Hymenoxys richardsonii	5	2 (40%)	
Salsola kali	7	3 (43%)	
Fendlera rupicola	2	1 (50%)	
Juniperus scopulorum	4	1 (25%)	1
Sphaeralcea	3	1 (33%)	
Marrubium vulgare	3	1 (33%)	
Ephedra viridis	3	1 (33%)	
Chrysothamnus nauseosus	7	2 (29%)	
Amelanchier	4	1 (25%)	
Gutierrezia	10	2 (20%)	
Artemisia ludoviciana	2		
Populus angustifolia	3		
Purshia tridentata	3		
Cercocarpus montanus	4		
Rhus trilobata	11		
(single occurrences grouped irrespective of preference)			
Sarcobatus vermiculatus	1	1	
Euphorbia serpyllifolia	1	1	
Smilacina	1	1	
Astragalus racemosus	1	1	
Chenopodium incanum	1	1	
Elymus macounii	1	1	
Mammillaria vivipara	1	1	
Lepidium	1	1	
Xanthium	1	1	
Prunus virginiana	1		
Acer negundo	1		
Salix	1		
Rosa	1		
Clematis ligusticifolia	1		
Forestiera neomexicana	1		
Ambrosia trifida	1		
Peraphyllum ramosissimum	1		
Eriogonum	1		
Artemisia frigida	1		
Agropyron smithii	1		
Sporobolus cryptandrus	1		
Hilaria jamesii	1		
Oryzopsis hymenoides	1		

N. albigula warreni

Among the most preferred food plants of *warreni* are tree cactus, one-seed juniper, *Yucca*, buffalo-bur, skunkbush, and Russian thistle. The succulent joints and fruits of tree cactus are eaten, and the spines are discarded. The seeds are also sometimes eaten, the split shells being discarded. Prickly pear cacti are eaten in much lesser amount than is tree cactus. Even when available, goldenrod, buckwheat, mugwort, snakeweed, and sunflower seem to be disliked.

Information concerning food is presented in the following paragraphs for each of 19 dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

Two Buttes Peak, 4500 Feet

9 May 1950.—500509-6. + *Yucca glauca*, * *Amaranthus retroflexus*, * *A. albus*, * *Solanum rostratum*, - *Opuntia humifusa*, - *Rhus trilobata*, -- *Kuhnia eupatorioides; Solidago, Cirsium, Buchloe dactyloides.* A large piece of prickly pear was in the nest chamber, but there was no midden of cactus spines. Remains of *Solanum rostratum* were the prickly fruit capsules. The sheltering thicket of skunkbush and separate soapweed plants had been pruned.

500509-8. + *Rhus trilobata*, * *Yucca glauca*, * *Bouteloua gracilis*, * *Sporobolus cryptandrus*, * *Solanum rostratum*, * *Artemisia* sp., - *Cirsium*, - *Salsola kali; Solidago, Artemisia ludoviciana mexicana.*

500509-11. * *Yucca glauca*, * *Artemisia* sp., * *Solanum rostratum*, - *Cirsium; Rhus trilobata, Solidago, Artemisia ludoviciana, Bouteloua gracilis, Sporobolus cryptandrus, Eriogonum.*

Two Buttes Reservoir, 4250 Feet

9 May 1950.—500509-12. + *Juniperus monosperma*, - *Yucca glauca*, - *Salsola kali*, -- *Oenothera lavandulaefolia*, -- *Asclepias arenaria*, -- *Psoralea; Eriogonum.* Green juniper cuttings amounted to more than 75 per cent of the food litter. Skunkbush grew 105 feet away from the den and was not utilized.

500509-13. + *Juniperus monosperma*, * *Yucca glauca*, * *Oenothera* sp., * *Salsola kali*, * *Solanum rostratum*, - *Cirsium*, - *Opuntia humifusa*, -- *Rhus trilobata*, -- *Eriogonum; Psoralea.* Rabbitbrush grew 120 feet away and was not utilized.

500509-14. + *Juniperus monosperma*, * *Yucca glauca*, * *Psoralea linearifolia*, * *Liatris punctata*, * *Cirsium*, - *Rhus trilobata*, - *Dalea aurea*, - *Salsola kali*, - *Bouteloua gracilis*, -- *Opuntia humifusa*, -- *Astragalus* sp., -- *Lesquerella ovalifolia*, -- *Mentzelia* sp., -- *Helianthus* sp., -- Cruciferae, -- *Ratibida columnifera; Tridens elongatus.* Remains of thistle were the dry seed-heads. Some soapweed plants had some of the leaf blades snipped off.

500509-15. + *Juniperus monosperma*, * *Artemisia ludoviciana*, * *Rhus trilobata*, * *Cirsium* sp., * *Liatris punctata*, * *Psoralea linearifolia*, - *Yucca glauca*, -- *Ambrosia coronopifolia*, -- *Oenothera* sp.; *Opuntia humifusa, Psoralea* sp. Juniper cuttings amounted to more than 80 per cent of the food litter.

One Mile North of Two Buttes Reservoir, 4350 Feet

11 May 1950.—500511-1. + *Yucca glauca,* * *Argemone platyceras hispida,* * *Helianthus* cf. *H. annuus,* * *Cirsium,* * *Bouteloua gracilis,* * *Solanum rostratum,* -- *Asclepias latifolia,* -- *Liatris punctata; Gutierrezia sarothrae, Opuntia polyacantha, Astragalus, Salsola kali.* Cactus was scarce at this locality; one *Opuntia polyacantha* grew 90 feet from the den. No cactus spines were noted in the middens or food litter.

One Mile Northwest of Higbee, 4200 Feet

16 May 1950.—500516-3. ++ *Opuntia arborescens,* - Lycoperdaceae, -- *Physalis; Opuntia humifusa, O. polyacantha, Helianthus, Cirsium, Melilotus, Sphaeralcea, Bouteloua gracilis.* More than 99 per cent of the food litter was from tree cactus, and the clump of cactus sheltering the den was extensively gnawed. In the midden, there were no spine-areoles.

500516-5. ++ *Opuntia arborescens,* - *Salsola kali,* -- *Asclepias arenaria; Juniperus monosperma, Opuntia humifusa, O. polyacantha, Yucca glauca, Helianthus, Cirsium, Bouteloua gracilis, Tridens elongatus.* More than 99 per cent of the food litter consisted of joints, fruits, and areoles of tree cactus. No pieces of soapweed were in the food litter, but some blades had been gnawed off a few growing plants.

500516-7. ++ *Opuntia arborescens; Opuntia humifusa, O. polyacantha, Gutierrezia, Yucca glauca, Helianthus, Salsola kali, Asclepias arenaria.* A hasty examination of the house revealed no food litter other than tree cactus.

500516-9. + *Opuntia arborescens,* * *Salsola kali,* * Graminae, -- *Opuntia humifusa; Juniperus monosperma, Opuntia polyacantha, Yucca glauca, Helianthus, Cirsium, Bouteloua gracilis.* Areoles and fruits of tree cactus comprised at least 75 per cent of the food litter. Split seeds of tree cactus were scattered in and in front of the nest of *Yucca* fibers. The nearest juniper stood 90 feet from the house.

500516-10. + *Opuntia arborescens,* - *O. humifusa,* - *Juniperus monosperma,* - *Yucca glauca,* -- *Opuntia polyacantha; Rhus trilobata, Atriplex canescens, Gutierrezia, Eriogonum, Artemisia ludoviciana, Helianthus.* Food litter was scanty. Tree cactus must have made up more than 50 per cent of the food. A clump of skunkbush screening the den was only slightly pruned.

500516-11. + *Opuntia arborescens,* * *O. polyacantha,* * *Juniperus monosperma,* * *Salsola kali; Rhus trilobata, Yucca glauca, Gutierrezia, Opuntia humifusa, Cucurbita foetidissima, Helianthus, Artemisia ludoviciana.* None of ten soapweed plants within 50 feet of the den had been pruned.

500516-13. + *Opuntia arborescens,* * *Juniperus monosperma,* * *Gutierrezia,* * *Rhus trilobata,* -- *Opuntia humifusa; Yucca glauca, Opuntia polyacantha, Salsola kali, Helianthus, Eriogonum.* More than 60 per cent of the food litter were areoles of tree cactus. Some soapweed plants near the house had been pruned, but no blades were seen in or on the house.

20 May 1950.—500520-2. + *Opuntia arborescens,* * *Juniperus monosperma,* * *Populus sargentii,* - *Salsola kali; Gutierrezia, Yucca glauca, Atriplex canescens, Opuntia polyacantha, O. humifusa, Cirsium, Astragalus?, Helianthus.* There were cottonwood twigs with the bark slightly gnawed and the petioles eaten and one leaf partly eaten.

Six Miles Northwest of Higbee, 4550 Feet

17 May 1950.—500517-1. + *Juniperus monosperma,* * *Yucca glauca,* * *Gutierrezia,* * *Salsola kali,* * *Helianthus,* * *Senecio,* - *Opuntia arborescens,* - *Asclepias latifolia,* -- *Opuntia humifusa; Artemisia* sp., *Eriogonum, Bouteloua gracilis.* The sheltering juniper was heavily pruned. The nearest soapweed plants were also extensively pruned. A few tree cactus areoles in the food litter must have been carried from plants more than 100 feet away.

500517-2. + *Juniperus monosperma,* + *Opuntia arborescens,* * *Salsola kali,* * *Senecio,* * *Psoralea* sp., - *Yucca glauca,* - *Artemisia* sp., - *Bouteloua gracilis,* - *Tridens elongatus,* - *Opuntia humifusa,* -- *Lesquerella fendleri; Gutierrezia, Mammillaria vivipara, Helianthus, Sphaeralcea, Eriogonum.* The nearest tree cactus grew 270 feet from the den. An isolated *Yucca* 120 feet from the den had many blades bitten off.

Seven Miles West and Two Miles North of Regnier, 4550 Feet

31 May 1951.—510531-1. * *Opuntia phaeacantha,* * *O. arborescens,* * *O. polyacantha,* * *Juniperus monosperma,* * *Pinus edulis,* * *Yucca* cf. *Y. standleyi,* * *Quercus undulata,* * *Rhus trilobata,* * *Mimosa borealis,* -- *Cercocarpus montanus; Opuntia humifusa, Bouteloua.*

A summary of food data obtained at all 19 dens of *N. a warreni* is presented in Table 27 in order to show the relative preference for each kind of food plant.

STORAGE

The storage habit of the white-throated wood rat is moderately developed, but food is seldom stored in large amounts, even in preparation for winter. Small supplies of food are apt to be found in the den irregularly at almost any time of year. The foods most commonly stored are joints and fruits of prickly pear and cholla cacti, foliage cuttings of juniper, and leaf blades of *Yucca.* Leaf cuttings of shrubs and forbs are sometimes stored.

The adaptive value of the storing instinct seems much less for *N. albigula* than for *N. cinerea* or *N. mexicana.* The winters at the lower elevations where *albigula* lives are less severe and snow cover is less prolonged than in the higher and colder habitat of *N. cinerea.* Also, the principal foods of *albigula* can be gathered at any season of the year. Perhaps the temporary storing in summer of foods that are high in water content enables the rat to have a continuously available supply of food and water under cover and thus avoid exposure to high temperatures.

One den of *N. albigula brevicauda* (490624-1) contained a substantial supply of stored food, consisting of dried and partly eaten joints of cactus *(Opuntia polyacantha* and *O. phaeacantha).* The joints were in two piles by two of the three nests in the house.

TABLE 27.—PLANTS AVAILABLE AND USED AS FOOD AT 19 DENS OF N. A. WARRENI (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE).

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Opuntia arborescens	9	11 (122%)	4
Juniperus monosperma	13	11 (85%)	4
Yucca	18	12 (67%)	3
Solanum rostratum	5	5 (100%)	
Rhus trilobata	9	7 (78%)	
Salsola kali	14	10 (71%)	
Liatris punctata	3	3 (100%)	
Oenothera	3	3 (100%)	
Asclepias	6	4 (67%)	1
Psoralea	6	4 (67%)	
Artemisia (shrub spp.)	4	3 (75%)	
Opuntia humifusa	15	8 (53%)	
Cirsium	11	6 (55%)	
Amaranthus	2	2 (100%)	
Senecio	2	2 (100%)	
Lesquerella	2	2 (100%)	
Bouteloua	10	4 (40%)	
Opuntia polyacantha	10	3 (30%)	
Sporobolus cryptandrus	2	1 (50%)	
Helianthus	12	3 (25%)	
Gutierrezia	8	2 (25%)	
Astragalus?	3	1 (33%)	
Tridens elongatus	3	1 (33%)	
Artemisia ludoviciana	5	1 (20%)	
Eriogonum	7	1 (14%)	
Atriplex canescens	2		
Sphaeralcea	2		
Solidago	3		
(single occurrences grouped irrespective of preference)			
Opuntia phaeacantha	1	1	
Pinus edulis	1	1	
Quercus undulata	1	1	
Mimosa borealis	1	1	
Argemone platyceras	1	1	
Dalea aurea	1	1	
Populus sargentii	1	1	
Kuhnia eupatorioides	1	1	
Ratibida columnifera	1	1	
Mentzelia	1	1	
Ambrosia coronopifolia	1	1	
Physalis	1	1	
Cercocarpus montanus	1	1	
Mammillaria vivipara	1		
Cucurbita foetidissima	1		
Melilotus	1		
Buchloe dactyloides	1		

Stored food material was found at 5 dens of *N. albigula laplataensis*, out of 13 dens examined. A vertical cleft at den 490827-1 was stuffed with 4 to 5 gallons of stored food, consisting of joints of rat-tail cactus and cuttings of scrub oak and winterfat. Den 491117-1 contained at least 12 green joints of cactus *(Opuntia rhodantha).* Den 491117-2 contained between 1 and 2 quarts of cuttings of Utah juniper scattered in the back of the den crevice.

Den 491024-1 contained within the den crevice many green joints of cactus *(Opuntia rhodantha* and *O. davisii).* In addition, one and a half gallons of cuttings of Utah juniper were under a large projecting boulder ten feet distant along the same ledge. Among the cuttings there were many bare uncracked nutlets, probably only as food debris left after the husks had been eaten from the juniper berries. At den 491024-8 there was approximately a gallon of mixed juniper cuttings (mostly *J. utahensis,* less *J. scopulorum)* inside an entrance; and elsewhere in the den there were 34 green joints of *O. rhodantha,* 20 of which were in one pocket.

Ten dens of *N. albigula warreni* contained storage, as described in the paragraphs below. The principal foods stored were joints and fruits of tree cactus, cuttings of juniper, and blades of soapweed.

Den 500509-6 contained at least a quart of cut pieces of the blades of soapweed and three fruit capsules of the same species in the nest chamber of the den. At den 500509-12 there were between 2 and 4 quarts of green cuttings of one-seed juniper filling crannies in various parts of the house. At den 500509-13 there was at least a gallon of cuttings, mostly of one-seed juniper, scattered throughout the house. At den 500509-15 there were approximately two quarts of cuttings of one-seed juniper scattered through the house. At den 500511-1 there were cut blades of soapweed scattered in the chambers and passages of the house. Perhaps these were merely for diurnal feeding.

In house 500516-7 there were approximately a quart of joints and a pint of dry fruits of tree cactus. House 500516-9 contained approximately a pint of fruits of tree cactus in masses of spine areoles. An undetermined quantity of joints and fruits of tree cactus were scattered inside house 500516-13. Nine fresh joints of tree cactus were around the nest of rat 500520-2 in a hollow cottonwood tree. House 500517-1 contained stored cuttings of one-seed juniper and soapweed amounting to approximately two gallons. The cuttings covered the floor of the lower central chamber and filled lateral recesses.

Bailey (1931: 179), speaking of *N. a. albigula* in New Mexico, reported ". . . along the lower slopes of the San Mateo Mountains [E. A. Goldman] was told that they gathered large quantities of pinyon nuts. A Mexican told him of gathering several bushels of these nuts by going from one house to another and robbing the storerooms in the interiors. He said that as much as 2 quarts were often found at one place." Vorhies and Taylor (1940: 522) attributed the same practice to the Navajo and other Indians, on the authority of Castetter (1935: 41), who wrote that the rats usually store 10 to 30 pounds of the seeds in a house. There is some uncertainty as to what species of wood rats provide such stores of piñon seeds. Examinations of dens in the present study do not support the above reports, but houses in suitable situations were too few to justify conclusions. Of the 17 dens of *N. albigula* examined where piñons were available, only two were houses that could be completely dismantled and searched for storage. No piñon seeds or debris of any kind were found at these two dens. The other 15 dens were among rocks that prevented access to all possible storage spaces.

REPRODUCTION AND YOUNG

An adult female *N. a. brevicauda* from one mile southwest of Gateway on 19 June 1949 was suckling two young that weighed 24.6 and 29.5 grams. Another old female caught the same day was also lactating, and a third female seemed to have recently ceased lactating. None had embryos. Two other adult females taken in June were neither pregnant nor lactating. An old adult male caught on 19 June had scrotal testes 15 mm long. He was probably still in active breeding condition. A subadult female from one mile northeast of Naturita weighed 74 grams on 26 June 1949 and was probably born in April.

Two records of embryos from Bedrock reported by Warren (1926: 98) under *Neotama mexicana fallax* are based on two females that are, in reality, *N. albigula brevicauda.* One with two embryos was caught on 16 April 1908, and the other with three on 17 April 1908.

A subadult male *N. a. laplataensis* from Bondad, 6050 feet, taken on 15 June 1949 weighed 106 grams. Two first year adults were taken at Four Corners on 25 July 1951. These rats were probably born in March or April. A first year adult female weighing 113 grams was taken on 15 September 1949 six miles east and 17 miles south of Cortez, 5600 feet. There are no records of pregnant females.

A high proportion of the females of *N. a. warreni* collected contained embryos or were lactating (see Table 28), owing to the coincidence that nearly all collecting of this subspecies was done in May or early June, which seems to be at the height of the breeding season. Out of 27 adult and subadult females collected by me, 21 were in breeding condition. Records of embryos indicated by asterisks in Table 28 were reported by Warren (1926: 98).

There are from 1 to 3 young per litter, usually 2. Three of the pregnant or lactating females listed in the table below were young adults born early the same year. They show that the breeding season begins much sooner than May and continues long enough for early-born females to reach maturity and bear young the same season. Some females probably bear two or more litters in a year.

Several subadult and adult rats of the year weighing from 94 to

TABLE 28.—BREEDING CONDITION OF FEMALES OF N. A. WARRENI

LOCALITY	Date	Age	Weight	Condition
* Irwin's Ranch..........	28 April	....	....	2 small embryos
Two Buttes peak, 4500 ft................	9 May	2nd year adult	220 g	lactating, no embryos
Two Buttes peak, 4500 ft................	9 May	3rd year sen.	270 g	3 embryos 38 mm
Two Buttes Reservoir, 4250 ft................	9 May	2nd year adult	164 g	2 embryos 17 mm
Two Buttes Reservoir, 4250 ft................	9 May	2nd year adult	193 g	uterus enlarged, full of jelly, no embryos
1 mi. N Two Buttes Reservoir, 4350 ft......	11 May	2nd year adult	202 g	lactating
1 mi. NW Higbee, 4200 ft................	16 May	2nd year adult	199 g	2 embryos 45 mm
1 mi. NW Higbee, 4200 ft................	16 May	2nd year adult	160 g	2 embryos 37 mm
1 mi. NW Higbee, 4200 ft................	16 May	3rd year adult	166 g	1 embryo 31 mm
1 mi. NW Higbee, 4200 ft................	16 May	2nd year adult	202 g	2 embryos 22 mm
6 mi. NW Higbee, 4550 ft................	17 May	2nd year adult	148 g	lactating, no embryo
1 mi. NW Higbee, 4200 ft................	20 May	3rd year senile	213 g	3 embryos 27 mm
* Gaume's Ranch.........	20 May	....	....	3 embryos
* Gaume's Ranch.........	22 May	....	....	3 small embryos
9 mi. SW Walsenburg, 6600 ft................	26 May	1st year adult	176 g	lactating, 1 suckling juv.
2 mi. E Wetmore, 5700 ft................	28 May	3rd year adult	245 g	2 embryos 18 mm
7 mi. W, 2 mi. N Regnier, 4550 ft................	31 May	2nd year adult	134 g	1 embryo 13 mm
7 mi. W, 2 mi. N Regnier, 4550 ft................	1 June	3rd year adult	204 g	lactating, no embryo
7 mi. W, 2 mi. N Regnier, 4550 ft................	1 June	2nd year adult	177 g	2 embryos 41 mm

TABLE 28.—*Concluded*

LOCALITY	Date	Age	Weight	Condition
Regnier, 4500 ft.	2 June	1st year adult	180 g	lactating, no embryo
2 mi. N Regnier, 4575 ft.	2 June	3rd year adult	203 g	lactating, 3 scars
2 mi. N Regnier, 4575 ft.	2 June	1st year adult	194 g	2 embryos
Regnier, 4500 ft.	2 June	1st year adult	162 g	2 embryos 8 mm
Regnier, 4500 ft.	2 June	2nd year adult	199 g	3 embryos 4 mm

194 grams were collected from 30 May to 2 June 1952, inclusive, at localities within ten miles of Regnier. An immature male and a subadult male weighing 58 and 70 grams, respectively, were caught one mile northwest of Higbee, 4200 feet, on 16 May 1950. All these specimens represent litters born in early spring.

On 30 May 1951, a first year adult male weighing 176 grams had enlarged testes and a second year adult male weighing 222 grams had testes 19 mm long. Both rats were trapped at the same den two miles north of Regnier, 4575 feet.

MOLTS

The general pattern of molts in *N. albigula* resembles that of *N. cinerea,* with a few differences. The postjuvenal molt lines from the sides join first on the lumbar region instead of on the rump, as in *cinerea;* and the same molt spreads over the inguinal region and inside of the thighs sooner than in *cinerea.* The second molt does not always begin before completion of the postjuvenal molt. In these respects the molt resembles the pattern seen in *N. floridana* and *N. micropus.*

Brief descriptions of some specimens in order of age are given below to illustrate significant stages in different molts and to show differences from the basic pattern described in more detail for *N. cinerea* (see p. 398). The seasonal distribution of specimens in molt is shown in Plate 22.

A subadult male *warreni* (DM1293) from Jimmie Creek, 20 May 1914, is in postjuvenal molt. Juvenal pelage covers the head, neck, and midline of the back and rump. Subadult pelage covers the belly, sides, legs, and hips. There is a distinct, concealed molt line on each side of the back, from each ear converging posteriorly to join at the lumbar region. From that point a narrow zone of short underlying subadult hairs covered by thin juvenal pelage extends 40 mm down the midline of the back to the rump, where separate molt lines diverge posteriorly. The middle of the rump is without sign of new hairs for a width of 9 mm. This molt pattern differs from that found in *N. cinerea*, in which the molt lines from the sides first join at the base of the tail instead of on the lumbar region or upper rump. The inguinal region and the inside of the thighs of DM 1293 seem to be in new pelage, and the lower legs in juvenal pelage. There is a molt line on each side of the neck below the ear, but none was found on the throat, breast, or face.

KU 34756, subadult female *brevicauda* from one mile northeast of Naturita, 26 June 1949, is unique in that the advanced postjuvenal molt line on the neck and upper back had come to a stop, except for a short line behind each ear formed by short subadult hairs concealed by juvenal hairs. Posteriorly from each patch of short hairs and across the back, full-length subadult pelage adjoins full-length juvenal pelage in a U-shaped line recognizable by differences in color and texture of the hairs.

A subadult male (KU 34766) from Bondad, 15 June 1949, is in postjuvenal molt which has been nearly completed, but no trace of the second molt was found on the abdomen.

A subadult taken on 11 June 1948, 14 miles north of Springfield, is in subadult pelage with the second molt just begun on the midline of the belly. This specimen and KU 34766 indicate that the postjuvenal molt is completed in some individuals before the second molt is begun. Such is not always the case, however, as shown by a first year adult female (KU 34762) from 5 miles east and 15 miles south of Mancos, 27 August 1949. The skin of this specimen shows the last remnant of the postjuvenal molt on the crown and a short "stubble" of first autumn hairs close against the skin over the midabdomen laterally to the lower sides and along the lateral line.

More advanced second molt is shown by a first year adult male (KU 29181) from 2 miles south and 4 miles west of Cortez, taken on 12 September.

An unusual variation of the molt pattern is shown by a first year adult female (KU 34757) taken on 15 September, 6 miles east and 17 miles south of Cortez. The second molt had spread less high up the sides than in the preceding specimen. However, a large separate area in the middle of the back had molted so that new pelage is visible there enclosed by sharply irregular concealed molt lines. On the rump there is an unusual wedge-shaped area of longer and yellower new pelage standing out sharply from the surrounding subadult pelage. The wedge-shaped area is delimited by a concealed molt line that spreads out posteriorly to join the normal molt lines on the hind legs. The area on the rump seems, in this specimen, to have been a separate center of molt, but normally in this species the rump is the last area to molt posteriorly by closing in of the lateral molt lines toward the base of the tail.

A second year adult male (DM 1291), from Jimmie Creek, on 20 May had begun annual molt over the area of the ventral dermal gland. A second year adult male (MVZ 61202), taken on 5 September nine miles west of the junction of the Purgatoire and Chacuaco rivers, is in a late stage of the annual molt. Most of the upper parts are molting irregularly or have completed molt.

PARASITES

The kinds of parasites collected from white-throated wood rats in the present study and the field numbers of individual hosts are listed below for each subspecies of wood rat.

Neotoma albigula brevicauda:

Trombiculidae

Trombicula potosina, 490619-6 & 7

Ceratophyllidae

Orchopeas sexdentatus, 890619-6

Neotoma albigula laplataensis:

Laelaptidae

Brevisterna utahensis, 490615-4

Trombiculidae

Euschöngastia lacerta, 490813-1
Trombicula (Eutrombicula) alfreddugesi, 490813-1
Trombicula potosina, 490813-1

Haematopinidae

Neohaematopinus neotomae, 490615-4

Hystrichopsyllidae

Anomiopsyllus sp., 490615-4

Ceratophyllidae

Malaraeus sp., 490615-3
Orchopeas sexdentatus, 490615-3

Neotoma albigula warreni:

Taeniidae

Cladotaenia sp., 500516-5 (cysticerci)

Ixodidae

Ixodes sp., 500509-6 (2 larvae)

Laelaptidae

Brevisterna utahensis, 500509-11, 500509-14, 500516-6

Trombiculidae

Euschöngastia criceticola, 500509-12, 500509-14
Trombicula arenicola, 500509-11

Haematopinidae

Neohaematopinus neotomae, 500509-6, 500509-8, 500509-11, 500509 12, 500509-14, 500511-1, 500516-5, 500516-6, 500516-7

Hystrichopsyllidae

Anomiopsyllus sp., 500516-5, 500516-6
Stenistomera alpina, 500509-6, 500509-11

Ceratophyllidae

Malaraeus sp., 500509-11, 500511-1

INJURIES AND DISEASE

Two skulls from 7 miles west and 2 miles north of Regnier are noteworthy for their dental abnormalities. A young adult male (KU 41065) has the dentine of the right M2 blackened and pitted by decay and the root partly loosened from the alveolus by an abscess. In the floor of the orbit an abnormally raised knob of the maxillary covers the root of the diseased M2. The left m2 is also partly decayed, but the alveolus seems to be normal.

A senile female (KU 41066) has an enlarged alveolar pit enclosing the posterior root of the right M1 and the anterior root of the right M2. In this pit at least ten cactus bristles are embedded between the teeth. There is no sign of tooth decay or abscess, other than the erosion or resorption of the alveolar margins to form the pit. Cactus bristles stuck between the molars and between alveoli and molars are of frequent occurrence in *N. albigula* and *N. micropus* and occur occasionally in wood rats of other species, in accordance with the relative abundance of cactus in the diet of the different species. However, this specimen (KU 41066) is the only one of *N. a. warreni* or *N. m. canescens* that I have seen in which the embedded bristles seem to have had any harmful effects on the teeth or jaws. Also, this specimen has the crown of the left M3 so badly decayed and worn down that only the neck of the crown remains holding the roots together.

Neotoma micropus Baird

Gray wood rat

HABITAT

The gray wood rat of the hot semiarid country of the southern High Plains and bordering deserts is at the northern limit of its range in southeastern Colorado. Its adaptations to desert life are similar to those of the white-throated wood rat, but the gray wood rat does not occur so high in the Upper Sonoran Life-zone; the highest record in Colorado is 5600 feet elevation, 11 miles north and 8 miles east of Branson. The highest record of *N. albigula warreni* is 6600 feet elevation, nine miles southwest of Walsenberg.

The tree cactus—short-grass community is the most favorable habitat in Colorado for the gray wood rat and nearly always supports a considerable population of this species if the rat is present anywhere in the area. The tree cactus *(Opuntia arborescens)* is a kind of cholla growing in the form of a large bush or dense clump of spiny branches reaching a height of 4 to 6 feet on favorable sites. It provides the wood rat with excellent shelter and an abundance of preferred food. Although the tree cactus occurs in other plant communities, such as the juniper—tree cactus community, *micropus* has not been found there, either because the range of *micropus* is less extensive or because the less abundant tree cactus in such other communities are already being used by *albigula*. For discussion of the relations between *micropus* and *albigula,* see pages 531 to 533. It is doubtful that the openness or grassy ground cover of the tree cactus—short-grass community are of any advantage to *micropus.* Rather, the luxuriance and abundance of tree cactus there more than compensate for the hazards of an otherwise inhospitable environment.

A basically similar habitat in which one den of the gray wood rat was studied is the yucca—short-grass community. This differs from the preceding primarily in the substitution of *Yucca glauca* for the tree cactus. Although the large clumps of yucca provide acceptable shelter and food, this plant is not nearly so favorable for *micropus* as the tree cactus. At a few localities this wood rat lives on rocky valley slopes or rims where the vegetation consists of a variety of mixed shrubs and prickly pear cactus. No single plant of the mixed shrub community has outstanding importance for the gray wood rat.

The dens studied of the gray wood rat were situated in the plant communities of the Upper Sonoran Life-zone as listed below:

Tree cactus—short-grass	6 dens
Yucca—short-grass	1
Mixed shrub	1

The topographic situations where *N. micropus* occurs depend upon the kinds of den shelter utilized. The rat is most numerous on alluvial fans because the tree cactus grows most abundantly on the well-drained gravelly soils on the alluvial fans. Other well-drained soils on the flanks of valleys, and sometimes even on higher slopes, support tree cactus and *N. micropus* in smaller numbers. Where yucca thickets are occupied these occur on the upland slopes of the High Plains. Rock dens are sometimes used by *micropus,* usually in crevices of rock ledges and outcrops on rocky canyon sides, or under large fallen blocks.

The dens studied of the gray wood rat are listed below by kinds of shelter and topography:

Shelter	*Topography*	*Number of dens*
Big sandstone block	Rocky canyon side	1
Tree cactus house	Alluvial fan	5
Tree cactus house	Sloping side of broad valley	1
Tunnels under yucca clump	Gently rolling plain	1

At several localities in southern Baca County gray wood rats were found, in 1951, only in tree cactus houses in tributary valleys of the Cimarron River. The tributaries flow south from the rim of the High Plains locally known as the "Cedar Breaks" or "Break-of-the-Plains." Seven miles west and two miles north of Regnier the sinuous rim of Dakota sandstone is rough, steep, and broken, but not quite cliff-forming (see Pl. 37, Fig. 1). The rim and steep rocky slope below support an open stand of one-seed junipers ("cedars"), piñons, and scattered shrubs—skunkbush, wavyleaf oak (*Quercus undulata* Torr.), mountain-mahogany, yucca, and prickly pear cactus. The lower gentle slopes of the valley leading west to Carrizo Creek are sparsely covered with grazed short grass, three kinds of prickly pear, and a few yuccas. Small alluvial fans on the sides of the valley support rather scattered but numerous tree cacti. Four gray wood rats were obtained from tree cactus houses on the alluvial fans, but extensive trapping among the rock ledges and boulders of the steep slope yielded only white-throated wood rats.

At Regnier, Colorado, by the Oklahoma state line, the valley of Gallinas Creek is deeper and the Dakota sandstone rim stands up as cliffs perhaps 20 to 40 feet high. Many clumps of skunkbush and only a few scattered junipers grow on the steep slopes below the cliffs. Numerous huge blocks of fallen sandstone dot the foot of the steep slope. The valley bottom is nearly flat and grass-covered with scattered soapweed. Cottonwoods grow along the creek. On an alluvial fan on the west side of the valley there are scattered tree cacti, from which I obtained a female *micropus* and three young by tearing open the house. Five *albigula* and two *mexicana* were trapped at dens under large sandstone blocks on the steep slope and at its foot. Three miles southeast of Regnier there were dens of this species in tree cactus houses on the gently sloping side of the wide Gallinas Valley near its confluence with the Cimarron Valley. Two miles north of Regnier many wood rats were trapped in 1951 along the irregularly broken rim of the High Plains, but all specimens were of *N. albigula warreni.* Their dens were in stick houses in juniper trees, under loose blocks, and in low clefts in the roughly eroded outcrops of Dakota sandstone.

In the shallow canyon of Chacuaco Creek, 11 miles north and 8 miles east of Branson, a few specimens of *micropus* were trapped at rock dens and a tree cactus house. The small canyon drains northward through the flat upland of the High Plains. As at Regnier, outcrops of the Dakota sandstone form the rim and steep sides of the winding valley. The stream bed switches from side to side between gently sloping and terraced bottomlands. The upland plains were covered with grazed short grass and scattered clumps of yucca. The rocky canyon sides were clothed in mixed shrubs, of which Rocky Mountain juniper, yucca, skunkbush, narrowleaf hoptree, and wavyleaf oak were the more abundant species. A few tree cacti grew there also, but these were much more numerous on the grassy bottomland, sometimes forming small dense thickets. Some yucca also grew on the bottomland.

Numerous wood rat houses were seen in the tree cacti, from which the only specimen taken was *micropus.* This species was trapped also at a den under one of the large sandstone blocks on the side of the valley. At a large den under a long horizontal ledge of rimrock, two adult rats trapped at opposite entrances proved to belong to *micropus* and *albigula.* It is an open question which rat lived in the den. Whether or not both species were occupying cactus houses, they were both using rock dens at this locality. A few other dens observed under rock shelter on the slope or canyon rim seemed to be of *N. mexicana,* but no specimens were obtained from them. These dens had some cactus but mostly small sticks and food cuttings of oak and hoptree.

The yucca—short-grass habitat in which a den of *micropus* was examined, as well as a den of *albigula,* is described on page 437.

In 1905 E. R. Warren collected at least 7 specimens of *micropus* at Monon. He found them "living among the sandstone rocks through which Bear Creek, in Baca County, has worn a channel. Here were many overhanging, shelving places, and cracks and crevices running back into the rock. About these places were found the messes of rubbish which it is the habit of all wood-rats, of whatever species, to collect about their nests and dens" (Warren, 1910: 109). His catalog and skin labels describe the locality as "Monon, J. M. Johnston Ranch" and "rocky bluffs by Bear Creek." The Johnston Ranch is on the north side of state highway 100 and the Santa Fe Railway. The farmer living just over the line in Kansas informed me (1951) that Monon was formerly a station where the Johnston Ranch headquarters stands. Concerning the gray wood rat, Cockrum wrote (1952: 190): "In Kansas this species builds its nests among rock ledges, and was extremely numerous along Bear Creek in western Stanton County in July, 1950. Here the nests were under ledges and in crevices of the rocks exposed on the southern side of the stream." Since Cockrum's locality is only about two miles down Bear Creek from Monon, it is probable that *micropus* was abundant also at Monon in July, 1950.

When I visited Monon on 29 May 1951 I found that the population of wood rats had been virtually wiped out by a great flash flood just two weeks before, which had inundated the entire valley and even some of the bordering upland fields. The low rocky bluffs on the east side of the creek bend north of the ranch house, probably the same ones where Warren caught *micropus,* were all topped by flood debris and a layer of silt (see Pl. 37, Fig. 2). On one of the ledges I found an old wood rat midden that had been covered with silt and almost obliterated except for a few projecting cactus spines. I explored both sides of the creek downstream into Kansas without finding sign of a single wood rat that might have survived the flood. The high water mark was everywhere above the outcrops of Dakota sandstone, which in this area does not form a valley rim but is overlain by the much softer Ogallala formation and associated soils. Willows in patches along the creek were mostly denuded and partly uprooted. Lower branches had been stripped off the cottonwoods, and many uprooted logs of these lay stranded on the edge of the plains. The plains upland just a few feet above the high water mark was grazed grassland, but elsewhere in Baca County much of the plains had been sown to wheat. Along the edges of the valley there were scattered yuccas and sand sage (*Artemisia filifolia*), locally abundant. Although the prospects for survival of wood rats looked so dim that I did not set any traps, it is not likely that every rat was killed by the flood. In a field of sand sage and yucca just above the flood line I tore open a wood rat house of cactus joints and sage sticks in a bush of sand sage but found no rat. At the edge of another field above the flood I saw some old rat sign in a pile of old lumber and trash. I turned over a number of boards without seeing any rat or fresh sign. Although adequate shelter above the flood was scarce, it seemed to be sufficient to permit the escape of a few individuals and future replenishment of the population.

DENS

Over most of its range, the gray wood rat builds houses of sticks, cactus joints and other material. Bailey reported such houses at numerous places in New Mexico (1931: 171-173) and in Texas (1905: 111-112). But in southwestern Kansas dens of this rat are more commonly found under rock ledges (Cockrum, 1952: 190) and in caves (Cockrum, verbal communication). In southeastern Colorado both kinds of dens are used. Warren collected *micropus* from dens among rock ledges at Monon (see p. 489). I examined numerous cactus houses on valley bottoms at several localities in Colorado. Although most of these houses were considerably smaller than the houses reported in New Mexico and Texas, the smaller houses were occupied by healthy adult rats. Since only one occupied den under rock shelter was examined in detail, no generalization concerning the preferred kinds of rock shelter can be offered. At most localities in Colorado where *micropus* was present, the steep rocky habitats were occupied by *albigula* and *mexicana* but not by *micropus.*

Houses of *micropus* in Colorado are usually low mounds, rarely as much as two feet high, and usually built around the base of a tree cactus, which provides some shelter and support. A wide smooth path ordinarily encircles the house, thus providing outside connections between the entrances to the house and from any entrance to any path leading away from the house. Most of the "ring path" is usually on bare soil but parts of it may cross accumulations of cactus spines or other midden material that has been pushed out of the entrances. The plan of the house is determined primarily by the features of the tree cactus. The basal branches of this cactus diverge from the stem at the ground level and serve as a natural division of the house into two levels, one above and between the basal branches, and the other below the ground surface under the branches and around the stem of the cactus. A house in poor condition may have the roof of the central chamber collapsed, or one or more chambers above ground may be filled with house debris or food litter and abandoned. In such a house the underground passages and chambers may be extended and constitute almost the entire serviceable part of the den. There is often an escape tunnel leading away from the lower level of the house.

These characteristics are the same as those of houses of *albigula* in tree cactus. The determining physical characteristics of the plant evoke the same responses from both kinds of rats. If, however, any other kinds of plant support were used by *micropus* in Colorado, as in New Mexico and Texas, the features of the houses would differ in many respects, depending on the physical properties of the sheltering plant.

Materials accumulated at dens, and the number of dens at which each occurred are as follows: livestock dung (mostly cattle), 8; joints and sticks of tree cactus, 7; joints of prickly pear *(O. phaeacantha)*, 2; small stones, 4; sticks of juniper and other shrubs, 3; stalks of sunflower and other weeds, 1; stalks of yucca, 1; small bones, 2; piñon cones, 1; black feathers, 1.

Nests of the gray wood rat have no features distinguishing them from those of all other kinds of wood rats. However, this species, more commonly than the others, seems to prefer an underground location. Since only seven nests were examined, it is not known whether the characteristics of these nests are generally typical for this rat. Two dens examined contained 2 nests each, and 3 dens contained 1 each. All the nests were underground, usually in a pocket opening on the ring passage. The only three nests whose shape I definitely determined were "semicup-shaped" or "semiroofed", that is to say, cuplike but with the back side built up higher than the front. Fine dry grass was the material commonly used, but two nests were made mostly of yucca fibers.

A cactus house of the gray wood rat was dismantled 7 miles west and 2 miles north of Regnier on 1 June 1951. The owner, a pregnant female (510601-6), was shot when exposed in an underground chamber. The house was built around the base of a tree cactus on a north-sloping alluvial fan. The habitat is described above on page 487. The supporting tree cactus was wide-spreading and nearly dead, with branches extensively gnawed and thinned out by wood rats. The house was a wide low mound of debris 15 inches in height, 60 inches in greatest diameter, and 39 inches in least diameter. The debris consisted mostly of dry joints of tree cactus with some cactus sticks. A large number of cakes of cow dung were incorporated in the roof of the house, which added greatly to its ability to shed rain. Other materials accumulated in the house in smaller amounts were juniper sticks, horse dung, piñon cones, a few prickly pear joints (*Opuntia phaeacantha*), and a few stones.

The living spaces within the house were arranged on two levels, one above ground and between the branches, and the other below ground under the basal branches. There were four entrances: one at each end (north and south), one multiple entrance on the east side, and one through a burrow on the southwest side. The north entrance opened upward on a ramp of cactus joints and areoles built up above ground like a dump of mine tailings. A peripheral ring path completely surrounded the house. On the uphill (south) side of the house a path led from the ring path away from the house to the next clump of tree cactus, which grew approximately 12 feet distant. That clump contained no wood rat den, and the cactus was more dense and healthy. A big wide midden of rat pellets lay outside the east entrance and was traversed by the ring path. Another fecal midden was on the floor of the upper level of the house. The roof of the house covered a large central chamber over this midden and between spreading and ascending branches of cactus. Secondary lateral branches provided additional support for the roof. The living space on the lower level of the house was essentially a ring of passages and chambers in the soil around the buried stem of the tree cactus; but the ring was not a closed circuit. One end of it opened up and out to the southwest entrance. The ring, after nearly encircling the stem, terminated at the other end in an underground chamber under the west side of the house. At the multiple entrance on the east side of the house there was an opening down into the lower ring and another upward directly into the main upper chamber. Two nests were found underground, one on the south side and the other on the northwest side. Both were made of fine dry grass and cup-shaped with the back side raised. There was no burrow leading away from the house or deeper underground by which the rat could escape or find more secure refuge.

Another cactus house, dismantled the following day in Oklahoma, just over the state line from Regnier, Colorado, contained a female (510602-12) and three suckling young. The habitat was a grassy alluvial apron on the side of the Gallinas Valley. The house was tidy and in good condition, but drainage was poor. Drift debris deposited by heavy runoff or sheet wash nearly touched the house. The latter was built mostly of joints and sticks of tree cactus. There were many pieces of cow dung, especially on the roof.

The house was 17 inches high, 57 inches long, and 42 inches wide. There were at least two entrances; other small openings may have been used as entrances less frequently. There was a good stand of grass close around the house and partly concealing a peripheral runway on the ground outside the house. Grass farther out from under the spreading branches of tree cactus had been closely grazed. Middens of food litter and fecal pellets were around the outside of the peripheral runway. The house contained spaces on two levels, one on the ground between the main cactus branches, and one sunk in the soil and covered with house materials. The sunken level was a ring of passages around the basal stem, with side pockets or chambers. In one of these side pockets there was a nest made of fine dry shredded grass. It was shaped like a cup with the back side raised. This den contained a good U-shaped burrow starting under the house, running west to a point two and one-half feet from the house and doubling back to emerge from the ground close to the house. The greatest depth of the tunnel was farthest from the house, where the bend was 14 inches below the surface.

A house in a tree cactus three miles southeast of Regnier, in Oklahoma, was essentially similar in plan and construction but was situated close to large patches of prickly pears (*Opuntia humifusa*) and had paths leading from the house into such a patch. The paths divided into a network of surface runways and burrows between and under prickly pears. Food litter, as in the case of all such houses of the gray wood rat, consisted mostly of joints and areoles of the tree cactus, but at this house there were also some partly eaten pieces of prickly pear.

A den of the gray wood rat was in a yucca thicket a mile north of Two Buttes Reservoir. An adult male (500510-2) was caught in a runway at this den. The habitat was a gently rolling plain and is described under the account of the white-throated wood rat (see p. 452). The den was situated on a gentle slope with fair drainage. The sheltering thicket of *Yucca glauca* was oval in outline and eleven feet long. It covered a low mound of soil, light brown sandy loam. The den consisted mainly of a network of burrows in the soil under the thicket. There was also a low, flat-roofed house hidden in the center of the clump of yucca. The house was composed of dry weed stalks and yucca blades (50± per cent), cow dung (40± per cent), and small amounts of yucca stalks, rabbit bones, and feathers. The house, covering an underground chamber, was dilapidated but the maze of tunnels and chambers elsewhere under the yuccas was neat. There were runways above ground under the spreading and drooping lower blades of the yucca plants. A nest made of yucca fibers was in a large underground chamber three feet from the low house. A second nest, abandoned, was in a chamber under yucca roots on the other side of the house. Approximately a quart of yucca blades cut for food lay scattered on the floor of the nest chamber in service. Most of the food litter was yucca debris and cactus areoles *(O. polyacantha).*

A protected den under a large block of sandstone rimrock (see Pl. 38, Fig. 1) was examined in the valley of Chacuaco Creek, northeast of Branson. A lactating adult female (500525-5) and a subadult male were trapped on the midden at this den on 25 May 1950. The habitat is described on page 488. Most of the sheltered living space of this den was inaccessible to me. The block of sandstone, approximately 15 feet long and 5 feet thick, rested on a moderate slope. The lower end of the block overhung a large midden of wood rat pellets and spiny areoles of tree cactus. Small amounts of other materials on or in the midden were small sticks and bones, a few pieces of cow dung, dry joints and a few sticks of tree cactus, and patches of old nesting material consisting of yucca fibers with some dry grass. It was estimated that more than 75 per cent of the food litter at this den consisted of areoles and gnawed joints of tree cactus.

FOOD AND STORAGE

The most important item of food used by eight *N. micropus* whose dens were studied was the tree cactus. At 7 of the 8 dens where tree cactus grew it was the most important single food plant, comprising more than three fourths of the food litter. The food debris consisted mostly of the spiny areoles from joints from which all succulent tissue had been eaten. Many green joints and partly eaten pieces of joints were left among the loose areoles. Dry uneaten joints of tree cactus were also abundant in the dens and were thought to be part of the protective den material, not food debris, although some may have been brought into the den when green. Spiny fruits were also eaten, but in much less quantity than the vegetative joints.

Six of the seven dens were situated in a bush or clump of tree cactus that provided the bulk of the den material as well as the food. The sheltering live cactus was nearly always heavily damaged by the gnawing and removal of joints. An occupied tree cactus could usually be recognized at a great distance by the thin open appearance of the upper part of the bush, even when the house at the base was not visible. Occasional plants were killed by the gnawing activities of the resident wood rat. Death of the cactus was usually followed by abandonment and decay of the house unless another live tree cactus was growing close by. The tree cactus is one of the few species of plants capable of providing nearly all of the needs of life for a wood rat. In this respect the tree cactus is as favorable to the gray wood rat as the coast live oak *(Quercus agrifolia* Née) is to the dusky-footed wood rat (*Neotoma fuscipes*) (Linsdale and Tevis, 1951: 21 and 305).

Tree cactus is not essential to the gray wood rat, although it is one of the most valuable food plants. One den was studied outside of the geographic range of tree cactus. The principal foods at this den were provided by *Yucca glauca* and *Opuntia polyacantha.* Of *Yucca* it was mostly the leaf blades that were eaten, but fruit capsules were gnawed and the seeds probably were eaten. The cactus food litter consisted of spines and partly eaten joints. It is noteworthy that where both tree cactus and *Yucca* were available, the wood rat ate little, if any, *Yucca.* Similarly, where both tree cactus and prickly pears were available, the prickly pears were eaten in slight to moderate amounts or not at all.

Food litter of other plants was composed mainly of leaf cuttings, twigs, and stems of shrubs and forbs from which most of the leaves had been eaten. A few acorns and winged seeds of *Ptelea baldwinii* were also eaten. Scattered stalks and seed heads of blue grama grass were sometimes left as food litter.

Thistles, skunkbush, *Hymenoxys richardsonii,* and *Astragalus?* or *Sophora?* are common plants in the range of *canescens* but seem to be disliked as food.

The food habits of *N. m. canescens* in Colorado scarcely differ from those of *N. albigula warreni.* Both kinds of wood rats subsist largely on the succulent joints of tree cactus or prickly pears when these are available, and neither has a geographic range extending outside of areas in which some species of cactus is abundant. Other kinds of food, such as *Yucca,* juniper, or leaves of shrubs suffice in the absence of cactus, but only as second-choice substitutes.

Information concerning food is presented in the following paragraphs for each of eight dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

One Mile North of Two Buttes Reservoir, 4350 Feet

10 May 1950.—500510-2. + *Yucca glauca,* + *Opuntia polyacantha,* * *Polanisia trachysperma; Gutierrezia, Bouteloua gracilis, Helianthus annuus, Cirsium, Astragalus?* or *Sophora?, Artemisia ludoviciana, Sphaeralcea, Argemone platyceras hispida, Salsola kali.* The nearest *Opuntia polyacantha* grew 25 yards from the den.

Eleven Miles North and Eight Miles East of Branson, 5600 Feet

25 May 1950.—500525-5. +*Opuntia arborescens,* * *Quercus undulata,* * *Juniperus scopulorum,* * *Opuntia polyacantha,* - *Ptelea baldwinii,* - *Yucca glauca,* - *Marrubium vulgare,* - *Salsola kali,* -- *Ribes cereum* or *inebrians,* -- *Xanthium; Rhus trilobata, Chrysothamnus, Artemisia ludoviciana, Gutierrezia.* Joints and areoles of tree cactus comprised about 75 per cent of the food litter. The nearest rabbitbrush and soapweed were 25 yards away from the den. A single cocklebur had been gnawed open and the seeds removed.

Seven Miles West and Two Miles North of Regnier, 4550 Feet

31 May 1951.—510531-7. ++ *Opuntia arborescens,* * Graminae; *Juniperus monosperma, Yucca glauca, Bouteloua gracilis, Cirsium, Astragalus?* or *Sophora?, Sphaeralcea, Ascelepias latifolia* or *arenaria.* A piñon pine stood at least 150 feet away from the den. The food litter consisted almost entirely of tree cactus areoles and joints.

1 June 1951.—510601-4. ++ *Opuntia arborescens,* * *Bouteloua gracilis,* - *Sphaeralcea; Yucca glauca, Opuntia humifusa, Opuntia polyacantha, Hymenoxys richardsonii, Astragalus?* or *Sophora?, Cirsium, Asclepias latifolia* or *arenaria.* The food litter consisted almost entirely of areoles and joints of tree cactus.

510601-3. ++ *Opuntia arborescens,* - *Bouteloua gracilis; Yucca glauca, Brickellia californica, Mimosa borealis, Rhus trilobata, Opuntia humifusa, Opuntia polyacantha, Hymenoxys richardsonii, Cirsium.* The food litter consisted almost entirely of tree cactus. The nearest skunkbush grew 90 feet away. Piñon and one-seed juniper were 50 yards away.

510601-6. ++ *Opuntia arborescens,* - *Opuntia phaeacantha,* * *Opuntia humifusa,* - Graminae; *Juniperus monosperma, Yucca glauca, Rhus trilobata, Hymenoxys richardsonii.* Cones of *Pinus edulis* may have provided food as well as den material. The cones must have come from trees more than 200 feet away.

Regnier, 4375 Feet, in Cimarron Co., Oklahoma

2 June 1951.—510602-12. ++ *Opuntia arborescens,* - Graminae, -- *Salsola kali,* -- *Asclepias latifolia?; Yucca glauca, Opuntia humifusa, Buchloe dactyloides, Cirsium, Sophora sericea.*

Three Miles Southeast of Regnier, 4350 Feet, in Oklahoma

2 June 1951.—510602-13. ++ *Opuntia arborescens,* - *Opuntia humifusa,* - Graminae; *Yucca glauca, Buchloe dactyloides.* Large patches of *Opuntia humifusa* were adjacent to the house, which was in a tree cactus, and provided shelter for a maze of tunnels immediately below the surface of the ground, but the *Opuntia humifusa* was only scantily used for food.

A summary of data on food obtained at 8 dens of *N. m. canescens* is presented in Table 29 in order to show the relative preference for each kind of food plant. High relative preference is indicated by high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants to the dens were also considered in arranging the plants roughly in order of decreasing preference. Only a few kinds of plants occurred often enough to show significant differences in preferences.

Three dens of *N. micropus canescens* contained small amounts of

TABLE 29.—PLANTS AVAILABLE AND USED AS FOOD AT 8 DENS OF N. M. CANESCENS (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Opuntia arborescens	7	7 (100%)	2
Opuntia polyacantha	4	2 (50%)	
Salsola kali	3	2 (67%)	
Opuntia humifusa	5	2 (40%)	
Bouteloua gracilis	4	2 (50%)	
Yucca glauca	8	2 (25%)	1
Sphaeralcea	3	1 (33%)	
Asclepias latifolia or *A. arenaria*	3	1 (33%)	
Juniperus monosperma	2		
Artemisia ludoviciana	2		
Gutierrezia	2		
Buchloe dactyloides	2		
Rhus trilobata	3		
Astragalus? or *Sophora*?	3		
Hymenoxys richardsonii	3		
Cirsium	5		
(single occurrences grouped irrespective of preference)			
Opuntia phaeacantha	1	1	
Quercus undulata	1	1	
Juniperus scopulorum	1	1	
Polanisia trachysperma	1	1	
Ptelea baldwinii	1	1	
Marrubium vulgare	1	1	
Ribes cereum	1	1	
Xanthium	1	1	
Helianthus annuus	1		
Chrysothamnus	1		
Brickellia californica	1		
Mimosa borealis	1		
Argemone platyceras	1		
Sophora sericea	1		

stored food for diurnal feeding, rather than seasonal use. A quart of cut blades of soapweed was on the floor of the nest chamber in house 500510-2. There were six green joints of tree cactus in a chamber of house 510531-7. House 510601-3 contained 15 green joints of tree cactus in the main chamber and underground tunnel.

REPRODUCTION AND YOUNG

An immature female and a subadult male were taken on 28 and 30 April 1905 at Monon. Several immature and subadult specimens were collected on 28 and 29 May 1938 at Furnish Canyon. In May, 1950, and early June, 1951, I collected six adult females, each of which was in breeding condition, as indicated in Table 30. Records of females with embryos reported by Warren (1926: 97) are included in the same table and marked by asterisks.

TABLE 30.—BREEDING CONDITION OF FEMALES OF N. M. CANESCENS

LOCALITY	Date	Age	Weight	Condition
11 mi. N, 8 mi. E Branson, 5600 ft.	25 May	2nd year adult	187 g	lactating, no embryo
11 mi. N, 8 mi. E Branson, 5600 ft.	25 May	2nd year adult	180 g	2 embryos 8 mm
Furnish Canyon	29 May	1st year adult	....	3 embryos
7 mi. W, 2 mi. N Regnier, 4550 ft.	1 June	2nd year adult	246 g	2 embryos 28 mm
7 mi. W, 2 mi. N Regnier, 4550 ft.	1 June	3rd year adult	241 g	2 embryos 8 mm
Regnier, 4375 ft., Okla.	2 June	3rd year adult	319 g	lactating, 3 suckling juv.
3 mi. SE Regnier, 4350 ft., Okla.	2 June	2nd year adult	313 g	3 embryos 20 mm
* Monon	28 April	....	....	3 embryos
* Monon	2 May	....	....	3 embryos

The breeding females and young rats recorded above indicate a rather long breeding season with the probability of two or more litters per year, under favorable circumstances. Young females born early in the year are capable of producing a litter by early summer of the same year. The normal number of young per litter seems to be 2 or 3.

A second year adult male taken on 31 May 1951, 7 miles west and 2 miles north of Regnier, 4550 feet, had testes 19 mm long, probably scrotal. A first year adult male, six months old when killed on 22 November 1951, had abdominal testes 15 mm long. He was caught as a suckling juvenile on 2 June 1951 at Regnier, 4375 feet, Oklahoma, and was reared in captivity at Lawrence, Kansas.

MOLTS

Nearly all specimens studied from Colorado were taken in spring or early summer. Hence the second molt is not represented. The principal difference seen between the molt cycle of *micropus* and that of *cinerea* is the presence of a time interval of full grown subadult pelage between the termination of the postjuvenal molt and the start of the second molt. Another difference is that the postjuvenal molt on the belly soon progresses backward over the inguinal region and inner sides of the hind legs, whereas the molt on the belly of *cinerea* is arrested and does not spread backward until the molt on the dorsum is nearly completed. The molt pattern of *micropus* most nearly resembles that of *floridana* and *albigula.*

The specimens mentioned below illustrate significant stages of molts and show differences from the basic pattern described in more detail for *N. cinerea* (see p. 398). The seasonal distribution of specimens in molt is shown in Plate 22.

DM 3237, a first year adult female barely past the subadult stage, from Furnish Canyon, 29 May 1938, has the postjuvenal molt far advanced, and sharply defined on the upper parts. The molt is in a narrow V-shaped pattern with the tip on the rump and the arms diverging to each shoulder. The space within the V and a spot at the base of the tail are in soft fuzzy juvenal pelage without sign of molt. Most of the rest of the upper parts are in full subadult pelage. Ventrally the molt has progressed posteriorly over the inguinal region and on the inner sides of the hind legs. There is a rather distinct V-shaped line across the breast separating thin soft hair on the throat and breast from thick straight stiffer hair on the abdomen. This line seems to represent the molt line, which had come to a halt long enough for the short new hairs to grow out to the same length as the old juvenal pelage. There is a separate area of molt on each cheek and side of the snout, separated from areas of new pelage on the neck and breast by areas of intervening juvenal pelage.

Two first year adults (DM 3236 ♂ and DM 3244 ♀) from

Furnish Canyon, 29 May 1938, and one (DM 3224 ♀) from Craugh Ranch taken the preceding day are in full subadult pelage with no sign either of the postjuvenal molt ending or of the second molt beginning.

DM 3241, second year adult male from Furnish Canyon, taken on 29 May, had begun to molt on the area of the ventral dermal gland, principally on the left side of the median line. This probably represents the onset of the annual molt. DM 3242, second year adult female, taken at the same place and on the same date, was molting heavily and irregularly over nearly all of the back, sides, and hips. Patches of new pelage contain new hairs varying from full length to the shortest "stubble". The nipples of this rat indicate she had only recently ceased lactating.

PARASITES

The kinds of parasites collected from gray wood rats in the present study and the field numbers of individual hosts are listed below.

Neotoma micropus canescens:

Laelaptidae

Haemolaelaps glasgowi, 510601-6, 510602-12, 510602-13

Trombiculidae

Euschöngastia criceticola, 500510-2

Haematopinidae

Neohaematopinus neotomae, 510602-12

Hystrichopsyllidae

Anomiopsyllus sp., 500510-2

Ceratophyllidae

Malaracus sp., 500510-2
Orchopeas sexdentatus, 510531-7, 510601-6, 510602-12, 510602-13

Neotoma floridana (Ord)

Florida wood rat

HABITAT

The Florida wood rat lives in a wide range of climate from the humid subtropical climate of the southeastern states to the semiarid temperate climate of the High Plains. On the plains of eastern Colorado the subspecies *N. f. campestris* represents an extreme of adaptation to the most arid conditions and coldest winters encountered by the species. Summers are generally dry and hot with temperatures frequently above 100° F. Winters are cold and dry with temperatures below freezing for long periods and occasional blizzards. Spring and fall are characterized by sharp and extreme changes in weather, strong winds, and dust storms in drier years. The range of *floridana* in Colorado is entirely within the upper Sonoran Life-zone and does not by any means cover all of that or even all of the plains portion of the Upper Sonoran. The highest occurrence of *floridana* seems to be 5700 feet elevation west of Fountain at the edge of the eastern foothills. Altitude and temperature are probably not appreciable factors limiting the spread of *floridana* in Colorado (see p. 543).

Kind of vegetation is not of much importance to the Florida wood rat. Almost the only limitation is that grassland alone is probably insufficient to fulfill its needs. Some kinds of shrubs, yucca, or tree cactus are always present and are used for food and sometimes shelter. The most commonly used plants are yucca, skunkbush, tree cactus, gray saltbush, and greasewood. Cottonwood trees are also used for shelter and food when available. The plant communities occupied are for the most part variants of the short-grass plains and the mixed shrub communities of the rocky gulches that cut through the plains.

The dens studied of the Florida wood rat were situated in the plant communities of the Upper Sonoran Life-zone as listed below:

Tree cactus—shadscale—short-grass	3 dens
Saltbush—grassland	2
Yucca—short-grass	1
Yucca—tree cactus—short-grass	1
Yucca—skunkbush	1
edge Yucca—short-grass and Mixed shrubs	1
Greasewood—tree cactus	1
Skunkbush—currant—grape	1
edge Rabbitbrush—grassland and Cottonwood	1

The ability of *floridana* to utilize either rock shelter, tree cactus, or large bushes for its dens enables it to occupy a considerable variety of landforms of low to moderate relief. But there seems to be a geographic difference in kinds of dens: in the northeastern part of its range *floridana* lives primarily in rock dens on the rims and steep slopes of gulches and river valleys of the Republican River drainage; in the southwestern part of its range, in the Arkansas River drainage, *floridana* lives almost entirely in houses built in the tree cactus or some large bush or thicket. This difference probably does not result from any difference in preference or capability of the wood rats, but only in distribution of kinds of shelter; for rock ledges are numerous in the northeast but large bushes and thickets

Fig. 1. Habitat of *N. albigula* in valley by John Brown Creek, one mile southwest of Gateway. The high cliff in the background is formed by Wingate sandstone, which in this area provides shelter for *N. cinerea.*

Fig. 2. North side of Mancos Canyon, 6 miles east and 17 miles south of Cortez. Dens of *N. albigula* and *N. mexicana* were numerous among rocks on the steep slope but absent on the valley floor.

PLATE 30

FIG. 1. East side of valley of Cherry Creek with low rim of sandstone outcrops providing ledges and crevices used by *N. albigula.* Den 491117-1 (see Pl. 31, Fig. 2) is under the long rock below the large piñon on the right.

FIG. 2. View north to Two Buttes, showing grazed short-grass plains and clumps of soapweed that sheltered houses and burrows of *N. albigula* and *N. micropus.* *N. mexicana* lived in rocks near the top of Two Buttes.

PLATE 31

Fig. 1. Entrance to den of N. *albigula* (480912-1) under large sandstone block 2 miles south and 4 miles west of Cortez. The opening has been nearly filled with sticks, dung, and cactus debris.

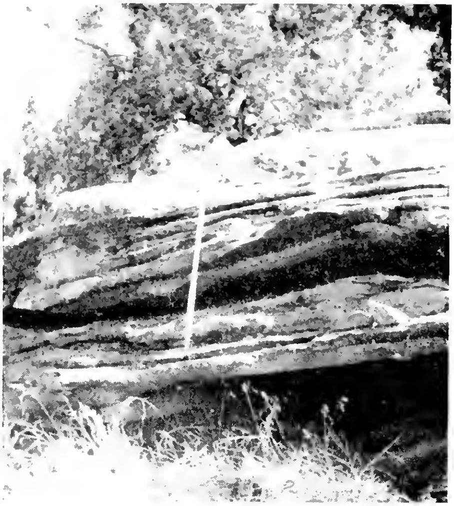


Fig. 2. Den of N. *albigula* (491117-1) in long horizontal crevice 5 miles east and 15 miles south of Mancos. (See valley slope shown in Pl. 30, Fig. 1.)

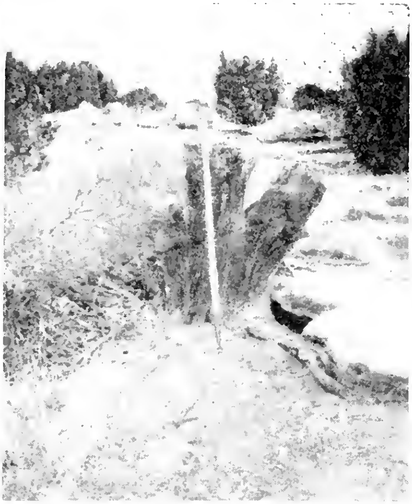


Fig. 3. Small den of N. *albigula* (500516-10) under rock slab one mile northwest of Higbee. Sticks were accumulated under the skunkbush to left of stump.

Fig. 1. House of *N. a. warreni* (500509-14) at Two Buttes Reservoir. The accumulation of sticks surrounds the basal branches of the one-seed juniper.

Fig. 2. House of *N. a. warreni* (500517-2) six miles northwest of Higbee. The crown of the house is supported by arching lower branches of the one-seed juniper.

PLATE 33

Fig. 1. House of *N. a. brevicauda* (490624-1) one mile southwest of Gateway. Nest A is in place, after removal of most of house crown. Materials consist mostly of livestock dung and sagebrush sticks. Six inches of the tape are extended.

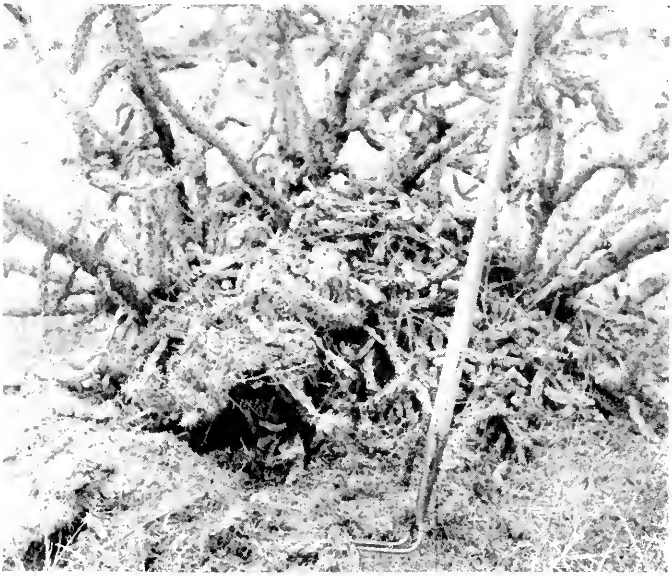


Fig. 2. House of *N. a. warreni* (500516-9) in base of tree cactus one mile northwest of Higbee. The two-pronged rake is an efficient tool for dismantling houses and retrieving objects from burrows or crevices.

PLATE 34

Fig. 1. Nest of *N. albigula* (500509-14) in place, in juniper house shown in Pl. 32, Fig. 1. The nest is semidomed, made of yucca fibers, and imbedded in midden beside an underground passageway.

Fig. 2. Nest of *N. albigula* (500509-6 and 7) in place, after removal of house, Two Buttes peak. Cut pieces of yucca blades cover the ground between nest and rock.

PLATE 35

Fig. 1. One-seed juniper sheltering a large house of *N. albigula* (500509-15), Two Buttes Reservoir. The rock bed of a shallow runoff channel surrounds tree and house.

Fig. 2. House of *N. albigula* (500511-1) in clump of *Yucca glauca*, one mile north of Two Buttes Reservoir. The habitat is shown in Pl. 30, Fig. 2.

PLATE 36

Fig. 1. Juniper with terminal branches stripped of needles by *N. albigula*, six miles northwest of Higbee. House 500517-1 is in base of juniper.

Fig. 2. Midden of cactus spine areoles at rock den of *N. albigula* (500525-10) northeast of Branson. The spines are food litter left from the consumption of large amounts of cactus pulp.

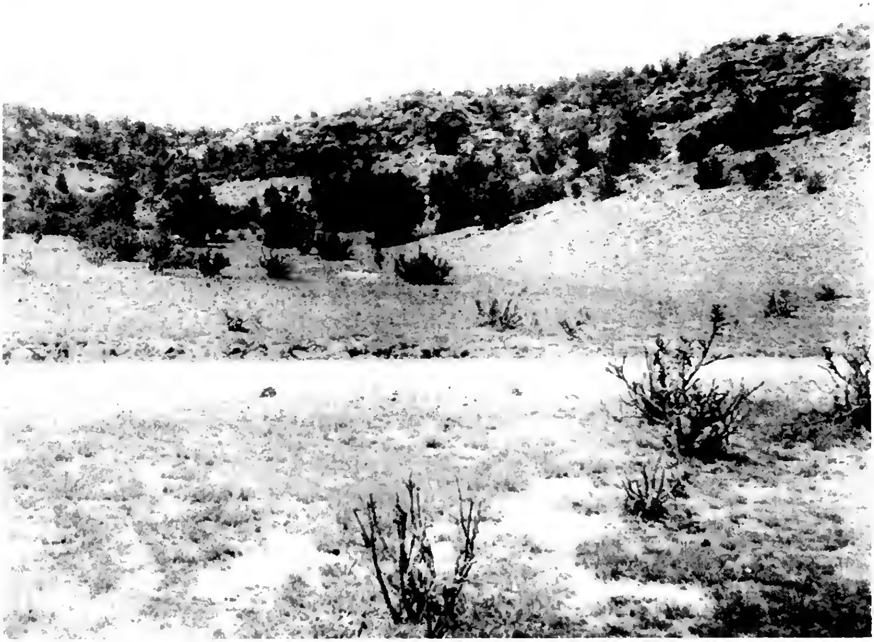


FIG. 1. "Cedar breaks" 7 miles west and 2 miles north of Reguier. *N. micropus* lived in tree cactus houses on the alluvial fan, and *N. albigula* lived in rock dens on steep slopes wooded with piñons and one-seed junipers.

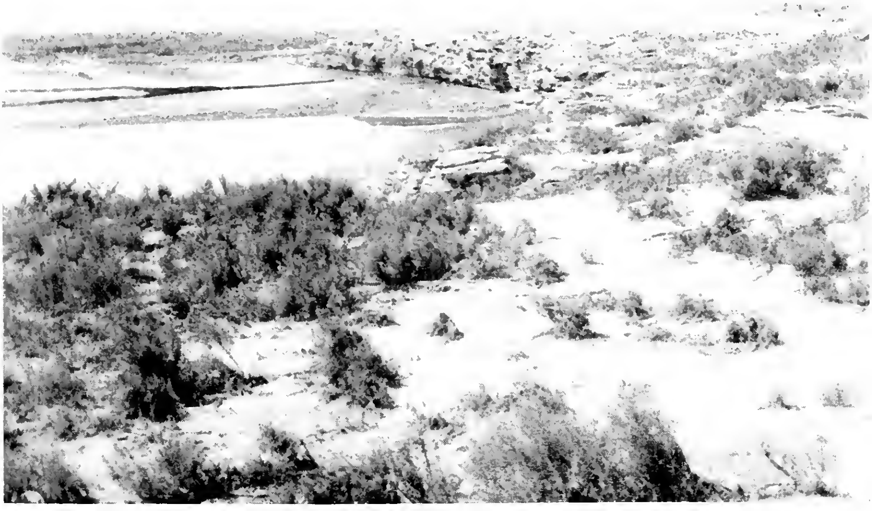


FIG. 2. Rocky bluff by Bear Creek north of Johnston Ranch house, Monon, on 29 May 1951. Gray wood rats living in rock dens were flooded out two weeks previously by a flash flood that deposited the layer of silt in foreground and over top of bluff.

FIG. 1. Den of *N. micropus* (500525-5) under fallen block of sandstone rimrock, 11 miles north and 8 miles east of Branson.

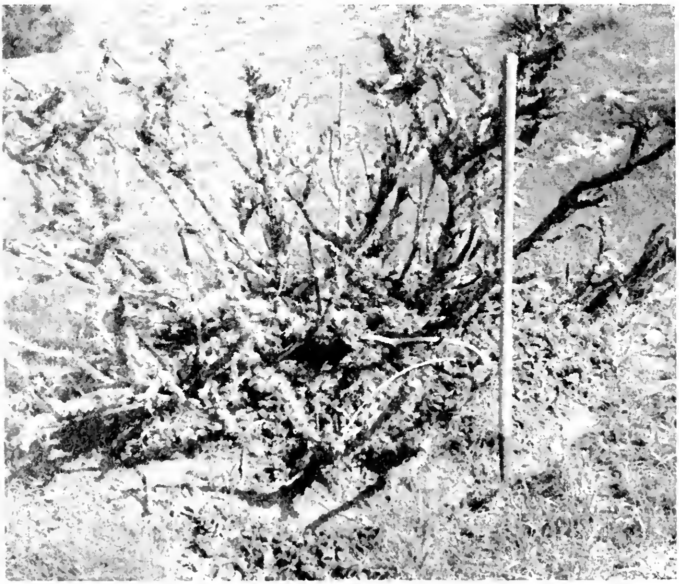


FIG. 2. Low house of *N. micropus* (510601-6) in base of tree cactus that had been nearly killed by gnawing of the wood rat, 7 miles west and 2 miles north of Regnier. Note peripheral ring path encircling house.

PLATE 39

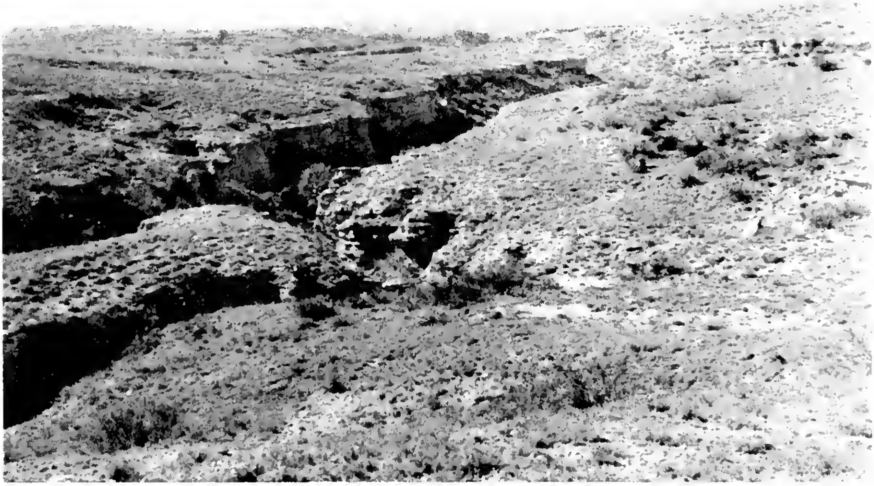


FIG. 1. Habitat of the Florida wood rat in a gulch cutting through the High Plains, one mile south of Wray; view northwest toward the Republican River.

FIG. 2. Rim outcrop around the head of a gulch one mile south of Wray. A den of *N. floridana* was under a limestone block in the thicket of mixed shrubs.

PLATE 40

FIG. 1. Soap weed (*Yucca glauca*) from which many leaf blades had been cut for food by *N. floridana*, one mile south of Wray.

FIG. 2. Pile of broken rimrock sheltering den of *N. floridana* (500603-1) in gulch one mile south of Wray.

PLATE 41

FIG. 1. House of *N. floridana* (500522-1) in shallow wash three miles north of Fowler. The tree cactus at left side of house probably had been killed by gnawing of the wood rat.

FIG. 2. Den of *N. floridana* (500529-3) in small pile of sticks and hollow log under cottonwood trees by Little Fountain Creek.

PLATE 42

FIG. 1. Habitat of *N. lepida* on rocky hill one mile southwest of Mack. View north showing Utah junipers in foreground and the Grand Valley in background.

FIG. 2. View west on hogback ridge south of Loma. *N. lepida* lives in rock crevices along crest of ridge and under fallen rocks on the slope.

FIG. 3. View northwest from same point on ridge, showing junipers on north slope, Uncompahgre Monocline in background, and the Grand Valley on right.

FIG. 1. Den of the desert wood rat (491110-2) under small boulder, with greasewood-covered valley floor south of Rangely in background.

FIG. 2. Sandstone blocks covering den of the desert wood rat (491110-3) on valley floor of West Fork of Douglas Creek, south of Rangely.

PLATE 44

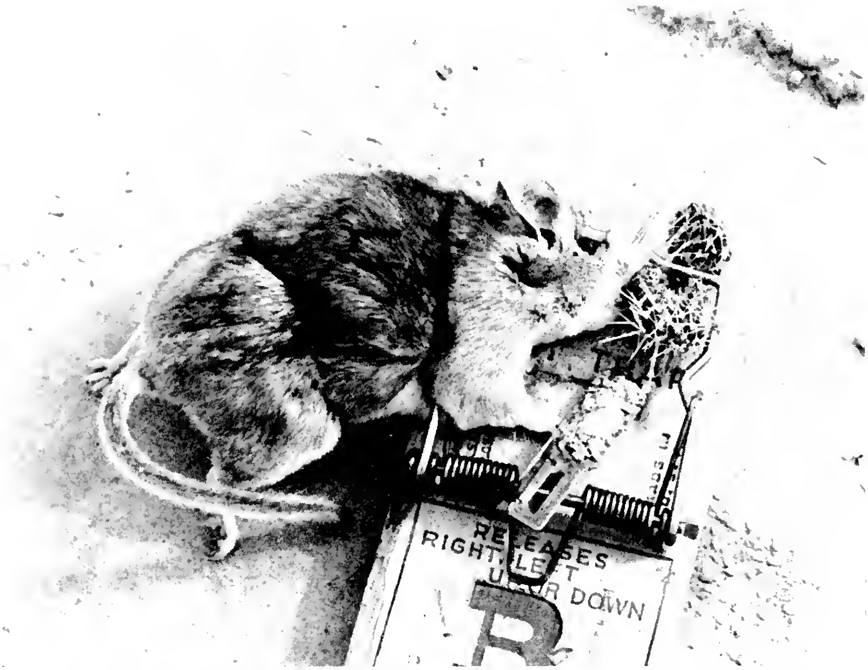


FIG. 1. Adult male *Neotoma lepida* (491110-3) caught while carrying a small cactus (*Opuntia polyacantha*) by the base.

FIG. 2. Den of *N. lepida* (491107-3) in crevices and behind loose block on crest of hogback ridge shown in Pl. 42, Fig. 2, south of Loma.

FIG. 3. End view of a large midden of *N. lepida* (491110-3) on a shelf under the huge sandstone blocks shown also in Pl. 43, Fig. 2.

are scarce, whereas in the southwest rock ledges are scarce but the tree cactus, saltbush and greasewood are abundant. Tree cactus, probably the favorite shrub for house construction, occurs north of the Arkansas River in only a limited area, roughly in the triangle of Las Animas—Fountain—Canon City.

The numbers of dens examined under each kind of shelter and in each topographic situation are presented in Table 31.

At Wray, where Warren and Cary also collected Florida wood rats, the rocky gulch habitat is well exemplified. The country around Wray is a flat and gently rolling plains upland which has been cut through from west to east by the small valley of the North Fork of the Republican River and its tributaries. On the north side of the river the valley is delimited by hilly slopes with few rock outcrops. But on the south side there is a rimrock of variable lithology forming low cliffs 6 to 20 feet high along the main valley and up the sides of tributary gulches to the south. The rimrock consists mostly of a friable silty and cherty limestone, gray or whitish in color. In some places outcrops of sandstone can be seen below the limestone. These are Tertiary continental sediments of the Ogallala formation, which blankets a large area of the High Plains along the eastern border of Colorado. Dens of wood rats were found only along rims and sides of the valley and tributary gulches where rock exposures provide natural shelter. They were more numerous toward the upper ends of tributary gulches than near or along the main river valley, mainly because large blocks of the Ogallala limestone that fall

TABLE 31.—SHELTER AND TOPOGRAPHY OF N. FLORIDANA

SHELTER	Topography and numbers of dens				
	Steep slope of gulch on plains	Gully or shallow wash on gentle slope	Foot of low hill by broad valley	Alluvial fan	Totals
Pile of rock slabs and blocks	1	......	......	......	1
Big block of cherty limestone	2	......	......	......	2
House on end of small rotten log	......	1	......	......	1
House in skunkbush clump	......	2	......	......	2
House in greasewood clump	......	......	......	1	1
House in saltbush	......	1	......	......	1
House between saltbush and tree cactus	......	1	......	......	1
House in tree cactus	......	......	1	2	3
Totals	3	5	1	3	12

farther downslope from the rim get broken up into so many pieces that they provide less shelter sufficient for wood rats. On the other hand, larger blocks of rimrock often slide intact into the heads of gulches and along the shallow upper portions of gulches.

Vegetation on the upland plain consisted of grazed short grasses, principally blue grama, and low matlike forbs and subshrubs such as *Hymenoxys scaposa.* In gulches the same grasses and other medium grasses grew, as well as many shrubs, and scrubby hackberry trees locally. The principal shrubs in the gulches were skunkbush, soapweed, and golden currant. In damper places such as the heads of gulches there were also chokecherry, grape, rose, snowberry, and *Rhus radicans.* Cottonwoods grew along the river bottom but not in the gulches. No wood rat dens were seen in shrubs or thickets or clumps of prickly pear away from rock shelter.

Houses in tree cactus and clumps of bushes were the characteristic form of den shelter on the north side of the Arkansas Valley three miles north of Fowler. The valley there was broad and shallow, and most of the bottom was irrigated farm land. The north rim of the valley was marked by the edge of the plains upland perhaps 100 feet above the valley bottom. The descent from upland to valley was by smoothly rounded bluffs or hillsides composed of unconsolidated gravel and silt probably a part of the Tertiary alluvial mantle. There were no outcrops of solid bedrock that could have provided any suitable rock shelter for wood rats. Along the base of the hillsides were alluvial fans that had coalesced to form a gently sloping apron flanking the hillsides and the cultivated bottomland.

The gravelly soil of the plains upland was only sparsely covered with short grasses (grazed), scattered tree cacti, and clumps of yucca. The same vegetation but fewer soapweed grew on the hillsides. On the gentle alluvial slopes at the foot of the hills and extending up into the gulches tree cacti grew larger and more numerous and there were many large bushes of gray saltbush. Grazed grasses and shadscale were the main ground cover. Tall dense clumps of greasewood grew on fallow land at the edge of the valley bottom and on the lower part of the alluvial apron. Throughout the area there were prickly pears of one or more species (*O. polyacantha, humifusa,* and *phaeacantha*).

On the alluvial fans, houses of the Florida wood rat were numerous in tree cactus, gray saltbush, and greasewood. Houses in tree cactus and saltbush were more scattered on the hillsides and gulches between the hills. On the upland there were a few houses in tree cactus, but a search for houses or sign in clumps of yucca was fruitless.

DENS

The Florida wood rat is one of the most versatile species in ability to make use of a wide variety of natural shelters and shelter materials. It is able to use a natural rock shelter or a hollow log or tree. When no rocks or trees are present it can build a substantial house in almost any thicket or dense bush or in a single isolated tree cactus. These capabilities enable the Florida wood rat to inhabit portions of the High Plains where resources suitable for wood rat dens are sparse at best.

Although rock dens of this species are characteristically under low ledge outcrops of sandstone or limestone or under fallen blocks, it is not correct to speak of any preference for such sites in contrast to large high clefts or caves in cliffs, since the Florida wood rat never finds the latter types of shelter within its range. The nearest mountainous terrain where such shelter could be found is already occupied by other species of wood rats.

Houses built by *floridana* in Colorado are not so massive as those built by the same species in the woods of eastern Kansas or those built by *fuscipes* in California (English, 1923: 2 & Pl. I; Vestal, 1938: 13-14; Linsdale and Tevis, 1951: 57-121). The materials used most by *floridana* are dry weed stalks, slender sticks, cow dung and cactus joints. Compared with the houses of *albigula* and *micropus*, those of *floridana* contain a much smaller proportion of cactus joints and spines, usually considerably less than 50 per cent. This is so, even when the house is in a tree cactus, unless no other suitable material is available. The utilization of tree cactus is sometimes sufficient, however, to damage seriously or kill the plant.

A typical house of the Florida wood rat is nearly or quite surrounded by a wide smooth path clear of spines or other debris but bordered by midden materials or quantities of cactus areoles. Most midden debris had been pushed outside of this "ring path" to form a sort of shoulder dump, like tailings from a mine. The path is sometimes partly overhung by the house, or by shrub branches. From this ring path usually two or more side paths lead away from the house to adjacent thickets and/or other wood rat houses. Sometimes paths connect three or more houses. Each house contains chambers and passageways on one or more levels above ground and usually one level partly or entirely below ground. One or two short escape burrows are sometimes present if the soil permits easy digging. The escape tunnel may open to the surface outside of the house or be merely a blind burrow, perhaps better called a refuge tunnel.

Materials accumulated at dens, and the number of dens at which each occurred are as follows: livestock dung, 11 (cattle 10, horse 1); sunflower stalks, 5; ragweed stalks, 3; other dry weed stalks, 6; joints and sticks of tree cactus, 6; joints of prickly pear, 4 (*O. polyacantha* 3, *O. humifusa* 1); sticks, 6 (skunkbush 3, greasewood 1, cottonwood 1); stones, 6; lumps of soil, 4; branches of Russian thistle, 4; branches of shadscale, 2; bones, 3; dry grass, 3; carnivore scats, 2; shotgun shells, 2; dry yucca blades, 1; cockleburs, 1; turkey wing-tip, 1; feathers, 1; big piece of wood rat fur, 1; orange rinds, 1; cardboard, 1; paper, 1; strip of red cloth (trap marker), 1; cotton work-glove, 1; blue medicine bottle, 1.

The nests of this wood rat are usually cup-shaped but may have the back side built up higher than the front making the upper part "semiroofed" or "semidomed". I found no completely domed or ball-shaped nests made by the Florida wood rat. A cup-shaped nest measured 5½ inches across the outside and 2½ inches across the inside. Yucca fibers are the nesting material most commonly used. The fibers are probably gathered from dead and rotting leaf blades of *Yucca glauca,* which abounds on the High Plains. Lesser amounts of fine dry grass are frequently incorporated in the nest, and occasionally the nest is composed entirely of grass. A single nest in a house by a cottonwood log was formed of shredded inner bark of the cottonwood. Materials found sporadically in small amounts were rabbit fur, feathers, shredded newspaper, and threads. In all, 17 nests were examined from 11 dens. No nest could be recovered from a twelfth den under rocks. Four dens contained 2 nests each and one contained 3 nests. Nests were found in various locations, both above ground in the houses and below in burrows.

A characteristic den under the shelter of rocks was examined in a rocky gulch one mile south of Wray, 3550 feet elevation. At this den an adult female (491123-1) was trapped on 23 November 1949. The habitat is described on page 501. The den was under a broken block of cherty limestone 12 feet long that rested at the top of the slope where it had broken off the rimrock. The block was partly imbedded in the ground and one end had broken into several pieces, between which was the main entrance to the den. The den was in good condition, tidy and with good shelter. Materials brought in by the rat were scarce, mostly scattered twigs, horse manure, and some dry brown weed stalks. The only woody plants within 100 feet of the den were soapweed, skunkbush, *Ribes*, and sand sage (*Artemisia filifolia*). Food litter was not abundant, being mainly twigs of skunkbush, and fruit capsules and pieces of leaf blades of *Yucca glauca.* Under the block were quantities of *Yucca* blades stored for food. The longest blade measured 23½ inches. I raked out and counted 236 pieces. Most blades had been cut into shorter sections. There was a nest of dry soft *Yucca* fibers under the main block. Plants from which many blades had been cut are shown in Plate 40, Figure 1.

Another den under a limestone block in the head of a gulch was the only one seen near Wray with a considerable accumulation of sticks. Although no rat was obtained at this den, the owner must have been *floridana,* the only species known from this locality. The block of rimrock was six feet high and nearly surrounded by a tangle of shrubs and vines (skunkbush, golden currant, grape, and snowberry). Two low piles of den material were under edges of the block and nearly concealed by the thicket. The den material consisted of sticks of skunkbush and other shrubs, a few cow chips, a few small bones and one *Geomys* skull. The main food litter consisted of many dry gnawed

Yucca pods and twigs of skunkbush, chokecherry, and golden currant. An old nest consisted of *Yucca* fibers mixed with dry grasses.

Houses supported by tree cacti were dismantled on the 21st and 22nd of May, 1950, three miles north of Fowler on the north edge of the Arkansas Valley. The habitat conditions at this locality are described on page 502. A good solid house was built in the center of a low, nearly dead clump of tree cactus on the alluvial apron fringing the low hills. Two subadults, including 500521-3, occupied this house, but no adult was seen. The tree cactus supporting this house had suffered so from the depredation of successive generations of rats that the plant was nearly dead and nearly all the central branches of the bush had been cut down. Only low, spreading, side branches remained alive. The conical house was 15 inches high, 70 inches long, and 50 inches wide. More than half of the building material consisted of small sticks, branches, twigs, and dry weed stalks (mostly sunflower). Smaller amounts of joints and sticks of tree cactus, cow dung, and gravel were also used. The principal kinds of food litter within the house were joints, fruits and areoles of tree cactus, and cuttings of saltbush and Russian thistle.

There were three entrances, all on or close to the ground level. Two entrances lead into a T-shaped passageway at the north end of the house. The entrance on the east side of the house was plugged with debris. Three fourths of the way around the house it was ringed by a smooth dirt path or runway 3 to 6 inches wide connecting the entrances. The path was clear of midden material, most of which lay outside of the path forming a sort of shoulder. The largest midden, three and a half feet long, fringed the southwest side of the ring path and was composed of earth, fecal pellets, and food litter. On the west side the path was screened by projecting sticks of the house, as well as spreading branches of the tree cactus. There was a large chamber in the north end of the house on sticks above the ground surface and the spreading basal branches of the tree cactus. Another large chamber in the south end of the house was in a depression excavated 6 to 8 inches below the ground surface. Below the north chamber an underground chamber had been excavated from which a blind tunnel lead off to the north. A similar underground chamber and tunnel with no outside exit underlay the south floor of the house. Two nests of yucca fiber were found, one in each of the underground chambers.

At a similar den (500522-6) in a clump of tree cactus an adult female was trapped and released alive. This den was noteworthy for the defunct condition of the main central chamber above ground. This had been abandoned and filled with food litter and den debris. Only the deeper and peripheral passages were still serviceable. It is also significant that the single nest excavated from a blind tunnel was composed mostly of yucca fibers, although the nearest yucca plant I could find was 50 yards away (paced). A wood rat will rarely go that far afield for food or den material if any usable substitute can be found nearer to its den.

An old, well-kept house (see Pl. 41, Fig. 1) was situated at the bottom of a little valley between the low hills, where an intermittent creek emerged from a small gully and aggraded the bottom with alluvial material. The drainage situation was poor because the lower edge of the house stood only 3 to 6 inches above the bottom of the shallow wash. Since even a small flash flood would make this house untenable, such floods from heavy thunderstorms must occur only at rare intervals of several years. The sparse rainfall that normally falls in this small drainage system probably sinks rapidly underground. The house stood between a large gray saltbush and a dead tree cactus, which probably was killed by the gnawing of the rat. An adult female (500522-1) was trapped at the house on 22 May 1950, and a juvenile with eyes closed was found in it.

Materials of the house were mostly dry sunflower stalks, with small sticks, cowchips, and a few stones and basal clumps of bunchgrass. Lesser items were a dry joint of *Opuntia polyacantha*, a few cockleburs, paper, and two shotgun shells with the paper casing gone. The house was 22 inches high, 58 inches long, and 48 inches wide. It had three active entrances, one on each side of the base of the dead tree cactus and one on the upper south side of the house by the saltbush. There were also two plugged entrances in disuse. A midden of food litter lay on the south side of the house below the high entrance. A large midden of food litter and rat feces was under the center of the house. One and a half feet north of the house, in front of a closed burrow, there was a big midden of mixed debris and earth. A ring path surrounding the house was clear and smooth on the south side of the house but not well cleared all around. There were two main living and feeding chambers centrally located under arching branches of the dead tree cactus which supported the stalks and other materials of the domed roof. One of the rooms was above the ground level and opened outside by the upper south entrance. The other room was partly below ground, in an excavated depression. The upper chamber contained fresh cuttings of greasewood and gray saltbush. The lower chamber contained freshly cut areoles of cactus, mostly of *Opuntia polyacantha*, but some of *O. arborescens*. In a pocket off the west side of the lower chamber there was a nest composed mostly of yucca fibers with some shredded newspaper mixed in. A burrow ran from the north end of the lower chamber under the roots of the tree cactus to the outside entrance one and a half feet north of the house. The entrance was plugged with a mass of cactus litter.

A few yards up the gully from the preceding den, a house stood on the rim and extended down over the bank to the bottom of the gully, which was two and a half feet deep. The owner was a pregnant and lactating female (500522-2). The house was supported by a clump of gray saltbush, some of the roots and branches of which were exposed and hanging down into the gully. In the upper part of the house and in the hanging part below the rim, there were chambers and passageways on four levels. Two nests of yucca fibers rested on the bottom of the gully against the bank and behind overhanging branches and den materials. Any appreciable flow of water down the gully would have made both nests unserviceable. House materials consisted of weed stalks, twigs, dry cactus joints, cow dung, stones, lumps of dirt, sticks of tree cactus and dry grass. Food materials on the floors of interior spaces were mostly joints and areoles of tree cactus and cuttings of gray saltbush.

Another den on the rim of a gully was studied one and a half miles southwest of Fountain, 5700 feet elevation. There was a low house in a skunkbush thicket. Two adult rats (500529-1♂ and 500529-2♀) were trapped at this house on 29 May 1950 and three nestlings with eyes still closed were found in the nest chamber when the house was dismantled. The gully, approximately five feet deep, ran northwest across a gently sloping plain flanking low rounded hills that fringed a higher plains-upland extending southward. The upland, hill slopes, and lower plains were covered with grazed short grasses and low forbs. *Yucca glauca* and tree cacti were scattered everywhere, but were more numerous on the steeper hill slopes and alluvial slopes between the hills. On the lower plain skunkbush grew in the form of low scattered bushes on the open grassland and small dense thickets on the banks of gullies. The thicket in which this house was situated was so dense that the house could only be seen by close inspection. Other plants nearby were a large thick bush of tree cactus, a clump of rabbitbrush, a wild gourd vine, ragweed (in gully), and Russian thistle. Materials comprising the house were mostly small sticks and twigs of skunkbush, a few stalks of ragweed, many rabbit and turkey bones, dry cow dung, many orange rinds, and a few carnivore scats. Food litter consisted mostly of cuttings of skunkbush with some of Russian thistle. Bark had been heavily eaten off the basal branches of skunkbush around which the house was built. Some branches had been girdled by the gnawing. The house extended down over the bank and had three levels and burrows into the bank. Two cup-shaped nests were in chambers at the ground level under overhanging branches on opposite sides of the house. One was made mostly of dry grass, with some yucca fibers. Rabbit fur and soft feathers were mixed in the lining. The second nest was of dry grass.

A den (see Pl. 41, Fig. 2) on the bank of Little Fountain Creek, 2 miles west and 3 miles south of Fountain was a small house of sticks heaped against one side of a log. On 29 May 1950 I caught an adult male (500529-3) at this den. The shallow creek valley, running eastward over the gently sloping upland plain, had a flat, partly wooded bottom and a meandering stream channel. The alkaline water in shallow pools left white powdery deposits on stones and mud banks. The den was on the south bank of the creek bottom. Cottonwoods (*Populus sargentii* and *P. acuminata*) there shaded the den part of the day. Small sprawling snowberry bushes were abundant under the cottonwoods. On the plain above the bank, only about six feet higher than the valley bottom, there were no trees, the highest vegetation being rabbitbrush, gray saltbush, and a few yuccas. Short grasses and hunger cactus also grew on the plain.

The house was at one end of the rotten cottonwood log and covered the space on the uphill side of it, so as to form a main chamber against the side of the log. The hollow interior of the log was also used as a passage and living space. Under the end of the log by the house, a low terrace on the back provided a partially sheltered spot where the rat might look out over the flat while feeding or resting. Below the terrace was a midden of litter and feces. Although the house was low and looked almost too small to be occupied, it was intact and tidy. It was composed mostly of sticks and bark of cottonwood. There were also many dry joints of hunger cactus and some dry ragweed stalks. A nest, semi-roofed in shape, was in the main chamber above the log. This nest is of particular interest, for it was the only one I found, made by any kind of wood rat, that was composed of the shredded inner bark of the cottonwood. There was a small proportion of dry grass and yucca fibers mixed in with the cottonwood bark.

By the same creek I set traps at another den, almost certainly of this species, but obtained no rat. This den was in holes under the roots of a cottonwood tree standing on the creek bank. In and below the entrances to passages under the roots, and in tunnels into the bank, there were many small cottonwood sticks and twigs that had all, or nearly all, the bark eaten off.

Lantz (Cary, 1911: 115) reported wood rats common in hollow cottonwoods along Big Sandy Creek near Hugo, Lincoln County. They would almost certainly have been of this species.

FOOD AND STORAGE

The succulent joints of cactus are an important part of the diet of the Florida wood rat in those parts of its range where cactus is abundant, such as in the upper Arkansas Valley within the range of the tree cactus. The leaves of shrubs are another important kind of food. Usually no single species of plant provides the great bulk of the food; the middens of food litter often are composed of a mixture of cactus areoles, gnawed joints and pieces of fruits of cactus, twigs and cuttings of leaves of shrubs, and scattered stalks and cuttings of forbs.

In the areas where rabbitbrush, sand sage, and *Hymenoxys scaposa* are available, these plants seem not to be well liked. Grasses are probably an insignificant part of the diet, at least in early summer. Flowers and fruits seem not to be a large part of the diet but probably become important in certain seasons. The dens examined in the present study are too few even to suggest the changing pattern of seasonal food preferences that must follow the vegetational changes.

Twelve dens of *N. f. campestris* were studied in Colorado. The studies provided information on some of the kinds of food eaten in different parts of the wood rat's range. The food records show a varied pattern of plant availability in different parts of Colorado and a corresponding flexibility in the diet of the wood rat. In the southwestern part of its range the tree cactus, greasewood, saltbush, and skunkbush were much eaten. Besides the leaves of the shrubs, considerable bark of greasewood and skunkbush was gnawed off the branches; sometimes branches within a house were girdled. Gnawed gourds of *Cucurbita foetidissima* were carried to dens from plants more than 100 feet away, but leaf cuttings were less used. At dens in Yuma County in the northeastern part of the wood rat's range, leaf cuttings of *Yucca glauca*, skunkbush, and chokecherry were important foods. Fruit capsules and seeds of *Yucca* were also eaten, and seed heads of sunflowers were collected, probably for the seeds.

N. f. campestris eats nearly the same kinds of plants as *N. albigula warreni* and *N. micropus canescens* but does not have such strong preference for cactus. Tree cactus and hunger cactus are much eaten but not so much as to produce a solidly intermeshed midden of cactus spines, as is commonly found at dens of the other two species.

The more abundant use of soapweed, skunkbush, and chokecherry by *floridana* reflects its Great Plains distribution and its lesser dependence on cactus.

Information concerning food is presented in the following paragraphs for each of 12 dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

One Mile South of Wray, 3500 to 3600 Feet

3 June 1950.—500603-1. + *Yucca glauca,* + *Helianthus annuus,* * *Prunus virginiana,* * *Mentzelia decapetala,* * *Amaranthus albus,* - *Rhus radicans,* - *Artemisia ludoviciana?,* - *Psoralea linearifolia,* -- *Senecio spartioides,* -- *Rhus trilobata,* -- *Rosa nutkana; Ribes aureum, Artemisia frigida, Celtis occidentalis, Vitis* sp., *Bouteloua, Hymenoxys scaposa.* The single scrubby hackberry tree had been heavily pruned, although no cuttings were seen at the den. *Yucca* and *Rhus radicans* had also been pruned.

500603-10 (den only). + *Yucca glauca,* * *Prunus virginiana,* * *Rhus trilobata,* * *Ribes aureum,* - *Vitis* sp., - *Rhus radicans,* - *Symphoricarpos* sp., - *Rosa nutkana; Hymenoxys scaposa.* There were many dry gnawed *Yucca* pods without seeds.

23 November 1949.—491123-1. + *Yucca glauca,* * *Rhus trilobata,* * *Helianthus annuus,* - *Kuhnia eupatorioides,* - *Opuntia polyacantha,* - *Gutierrezia; Artemisia filifolia, Ribes* sp., *Artemisia frigida, Polanisia trachysperma, Hymenoxys scaposa, Bouteloua.*

Three Miles North of Fowler, 4400 Feet

21 May 1950.—500521-1 & 2. + *Opuntia arborescens,* + *Atriplex confertifolia,* - *Yucca glauca,* - *Opuntia polyacantha; Chrysothamnus nauseosus, Salsola kali, Helianthus, Mammillaria vivipara, Bouteloua, Tridens elongatus.* Joints, fruits, and areoles of tree cactus made up at least 60 per cent of the food material.

500521-3. + *Atriplex confertifolia,* * *Opuntia arborescens,* * *Salsola kali,* * *Cucurbita foetidissima,* * *Grindelia* sp.; *Opuntia polyacantha, Opuntia humifusa, Helianthus, Bouteloua, Tridens elongatus.* Clumps of greasewood were growing 50 yards from the den.

500521-4. + *Sarcobatus vermiculatus,* + *Ambrosia* sp., + *Opuntia arborescens,* - *Cucurbita foetidissima,* - *Salsola kali; Atriplex confertifolia, Yucca glauca, Artemisia filifolia, Chrysothamnus nausosus, Opuntia phaeacantha.* Greasewood, ragweed, and tree cactus debris each comprised about 30 per cent of the food litter.

22 May 1950.—500522-1. + *Opuntia polyacantha,* * *Opuntia arborescens,* * *Sarcobatus vermiculatus,* * *Atriplex canescens,* - *Salsola kali,* - *Gutierrezia,* - *Sporobolus airoides; Atriplex confertifolia, Chrysothamnus nauseosus, Yucca glauca, Astragalus?, Helianthus, Tridens elongatus.* Bark had been eaten off freshly cut greasewood twigs and branches in the house. The nearest tree cactus and soapweed were growing 25 yards from the house.

500522-2. + *Opuntia arborescens,* + *Atriplex canescens,* * *Chrysothamnus nauseosus,* * *Opuntia humifusa,* * *Opuntia polyacantha,* - *Yucca glauca; Gutier-*

rezia, Astragalus?, Tridens elongatus, Sporobolus airoides, Bouteloua. Shadscale was growing 35 yards from the house. The nearest tree cactus was 25 yards away, and the nearest soapweed was 20 yards away.

500522-6. * *Opuntia arborescens,* * *Salsola kali,* * *Cucurbita foetidissima,* - *Atriplex confertifolia,* - *Bouteloua gracilis; Helianthus, Opuntia polyacantha, Opuntia humifusa, Chrysothamnus nauseosus, Atriplex canescens, Sarcobatus vermiculatus, Artemisia filifolia, Tridens elongatus.* Three pieces of gourds must have come from at least 40 yards away, the distance to the nearest *Cucurbita* plant. The nearest greasewood and sand sage grew 80 feet from the den.

One and One-half Mile Southwest of Fountain, 5700 Feet

29 May 1950.—500529-1. + *Rhus trilobata,* * *Salsola kali,* - *Opuntia arborescens,* - *Ambrosia* sp., -- *Cucurbita foetidissima; Yucca glauca, Chrysothamnus* sp., *Gutierrezia.* Bark had been extensively eaten off the basal branches of skunkbush, and some of these branches were girdled.

Two Miles West and Three Miles South of Fountain, 5600 Feet

29 May 1950.—500529-3. + *Opuntia polyacantha,* * *Populus sargentii,* * *Populus acuminata,* - *Stanleya pinnata; Chrysothamnus nauseosus, Atriplex canescens, Symphoricarpos* sp., *Clematis ligusticifolia, Ambrosia, Yucca glauca.* Food litter from the two kinds of cottonwoods present consisted of partly-eaten leaf cuttings of the plains cottonwood and unidentifiable cottonwood sticks with bark eaten off, probably of both species.

Two and One-half Miles Southwest of Fountain, 5700 Feet

30 May 1950.—500530-1. + *Rhus trilobata,* * *Opuntia arborescens,* * *Yucca glauca,* - *Opuntia humifusa,* - *Artemisia ludoviciana,* - *Mentzelia* sp.; *Chrysothamnus, Symphoricarpos* sp., *Psoralea* sp., *Ambrosia, Eriogonum, Salsola kali, Gutierrezia, Helianthus.*

A summary of data on food obtained at 12 dens of *N. f. campestris* is presented in Table 32 in order to show the relative preference for each kind of food plant. High relative preference is indicated by high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants to the dens also were considered in arranging the plants roughly in order of decreasing preference.

Stored food material was found at four dens of this species. At den 491123-1 under a fallen block of rimrock, 236 fresh pieces of blades of *Yucca glauca* were recovered from under the block, by raking them out of two entrances. From one entrance 204 pieces were obtained, and from the other, 32 pieces. The longest blade was 23½ inches long. In June at den 500603-1 an old supply of *Yucca glauca* blades, probably dating from the previous autumn, was found buried under a piece of rimrock. At den 500521-4 in May there was approximately a quart of ragweed cuttings crammed

TABLE 32.—PLANTS AVAILABLE AND USED AS FOOD AT 12 DENS OF N. F. CAMPESTRIS (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Opuntia arborescens	8	8 (100%)	
Rhus trilobata	5	5 (100%)	
Cucurbita foetidissima	2	4 (200%)	
Opuntia polyacantha	7	5 (71%)	
Yucca glauca	10	6 (60%)	2
Salsola kali	7	5 (71%)	
Prunus virginiana	2	2 (100%)	
Mentzelia	2	2 (100%)	
Rhus radicans	2	2 (100%)	
Artemisia ludoviciana?	2	2 (100%)	
Rosa nutkana	2	2 (100%)	
Sarcobatus vermiculatus	3	2 (67%)	
Atriplex confertifolia	6	3 (50%)	
Atriplex canescens	4	2 (50%)	1
Ambrosia	4	2 (50%)	1
Opuntia humifusa	4	2 (50%)	
Populus	2	1 (50%)	
Psoralea	2	1 (50%)	
Vitis	2	1 (50%)	
Sporobolus airoides	2	1 (50%)	
Gutierrezia	5	2 (40%)	
Ribes	3	1 (33%)	
Helianthus	7	2 (29%)	
Symphoricarpos	3	1 (33%)	
Chrysothamnus	7	1 (14%)	
Bouteloua	6	1 (17%)	
Artemisia frigida	2		
Astragalus?	2		
Artemisia filifolia	3		
Hymenoxys scaposa	3		
Tridens elongatus	5		
(single occurrences grouped irrespective of preference)			
Amaranthus albus		1	
Grindelia squarrosa?		1	
Senecio spartioides		1	
Stanleya pinnata	1	1	
Kuhnia eupatorioides	1	1	
Opuntia phaeacantha	1		
Celtis occidentalis	1		
Clematis ligusticifolia	1		
Eriogonum	1		
Mammillaria vivipara	1		
Polanisia trachysperma	1		

among sticks in the top of the wood rat house. At den 500522-2 there was approximately a quart of dry green saltbush cuttings in chambers in the house. These observations indicate that the storage habit is moderately well developed in *N. f. campestris.*

REPRODUCTION AND YOUNG

Some females bear more than one litter per year in the spring and early summer. An immature female weighing 81 grams was taken on 3 June 1950, one mile south of Wray, 3600 feet. In addition to the four adult females in breeding condition listed in Table 33, I collected three that were not in breeding condition, two of which were taken in late May and early June and the third on 23 November.

TABLE 33.—BREEDING CONDITION OF FEMALES OF N. F. CAMPESTRIS

LOCALITY	Date	Age	Weight	Condition
3 mi. N Fowler, 4400 ft.	21 May	2nd year adult	241 g	lactating, no embryo
3 mi. N Fowler, 4400 ft.	22 May	2nd year adult	263 g	lactating, no embryo
3 mi. N Fowler, 4400 ft.	22 May	3rd year adult	342 g	lactating, 4 emb. 20 mm
1½ mi. SW Fountain, 5700 ft.	29 May	3rd year senile	329 g	lactating, 2 suckling juv.

MOLTS

Molts in *N. floridana* were difficult to trace because summer-taken specimens were scarce. The skins available from spring and autumn conform, in general, with the patterns of molt described for *N. cinerea* (see p. 398). Minor differences from *cinerea* are the relatively early progression of molt over the inguinal region in *floridana* and the joining of postjuvenal molt lines from opposite sides on the lumbar region instead of on the rump. The seasonal distribution of specimens in molt is shown in Plate 22.

The earliest stage of the postjuvenal molt illustrated by specimens at hand is seen in KU 37095, young subadult male, from three miles north of Fowler, 21 May 1950. The upper parts are entirely covered by soft gray juvenal pelage. Short new subadult hairs are coming in on the sides, hips, and hind legs. In a zone across the lumbar region, new hairs have just emerged from the skin, but on the rump there is a median area with no trace of new hairs. The new pelage is about two thirds the length of the juvenal pelage on the lateral line, and full length on the abdomen. Short subadult hairs are growing over the inguinal region, which does not normally molt in *N. cinerea* until the molt on the dorsum is more advanced. The anterior limit of molt is a V-shaped line across the throat and up the sides of the neck to the ears.

The last trace of the postjuvenal molt, simultaneously with the second molt, is shown by ClMNH 12323, first year adult male, from ten miles south of Colorado Springs, 6 September 1937. Although the molars of this specimen are fully mature, the exoccipital sutures are still visible and the maxillary branch of the zygomatic arch is incompletely ossified, as in subadult skulls. The upper parts are entirely covered with short smooth subadult pelage, except for a small thin remnant of juvenal pelage on the nape overlying the two-thirds grown subadult pelage. Short hairs of the first autumn pelage underlie the subadult pelage on the sides and hind legs and merge with full-length, first autumn pelage covering the belly. Concealed second molt lines cross the inguinal region and breast between the axillae.

Two first year adult males from Olney give evidence of a third molt in the first year. Both are large adult rats. BSC 69941 male, taken on 5 December, shows two molts. An earlier band of molt crosses the upper back and dwindles out at each end behind the shoulders, as though the molt line above each shoulder had halted long enough for the new hairs to grow out to full length. This must be a late stage of the second molt. Along each side just above the lateral line is a later narrow molt line, visible when the fur is parted. This is the third molt of the year, which replaces the first autumn pelage with the first winter pelage.

No Florida wood rats in full annual molt are available from Colorado. AM 28174, second year adult male, from Wray, 5 March 1907, had started to molt on the belly over the area of the ventral dermal gland. Perhaps this represents the beginning of the annual molt at what seems to be an unusually early date. KU 34747, second year adult female, from Wray, 23 November 1949, has long thick pelage with a zone of thin molt along each lateral line. Over the entire back the fur, when separated, has a double-banded appearance, as though the new pelage has not quite grown out to full length. This rat probably is in the last stages of the annual molt.

PARASITES

The kinds of parasites collected from Florida wood rats in the present study and the field numbers of individual hosts are listed below.

Neotoma floridana campestris:

Laelaptidae

Brevisterna utahensis, 500521-3
Haemolaelaps glasgowi, 500521-3

Trombiculidae

Euschöngastia criceticola, 491123-1, 500521-1

Haematopinidae

Neohaematopinus neotomae, 500521-1, 500521-3

Hystrichopsyllidae

Anomiopsyllus sp., 500521-3, 500521-4
Stenistomera alpina, 500603-1

Ceratophyllidae

Malaraeus sp., 500521-4
Orchopeas sexdentatus, 500521-1, 500521-3

Neotoma lepida Thomas

Desert wood rat

HABITAT

The desert wood rat, as its name implies, lives primarily in desert or semidesert habitats of the Southwest. In Colorado it has been found only in the Upper Sonoran Life-zone and, to the best of my knowledge, not so high as its upper limit. The highest altitude record is 6200 feet on the West Fork of Douglas Creek. There and throughout much of the northerly range of the species in Utah and Nevada the winters are moderately cold with snow.

Most of the dens seen of this species were in plant communities dominated by juniper or shadscale or some combination of these and other plants. About half of the dens studied were within 100 feet of Utah junipers, but these trees were more scattered than in the juniper—piñon scrub forest of higher elevations. The lowest occurrence of piñons near desert wood rat dens studied was on the top of the ridge south of Mack where there were scattered piñons among junipers. Shadscale is the only conspicuous plant recorded within 100 feet of all dens examined. Only in the greasewood—grassland community was cactus fairly common close to the dens.

The dens studied of the desert wood rat were situated in the plant communities of the Upper Sonoran Life-zone as listed below:

Juniper	2 dens
Juniper—sagebrush	1
edge Juniper—sagebrush and Shadscale	1
Juniper—shadscale	1
Shadscale	1
Shadscale—Russian thistle	1
Grassland—scattered greasewood	2

All dens that I found were associated with rocks, usually sandstone outcrops and ledges, or fallen boulders, slabs, or huge blocks. A few dens were in vertical or diagonal crevices in low cliffs. Cary reported catching desert wood rats at houses made of cow dung and cactus joints (see p. 519). The dens that I studied are listed in Table 34 by kinds of shelter and kinds of topography.

TABLE 34.—SHELTER AND TOPOGRAPHY OF N. LEPIDA

SHELTER	Topography and numbers of dens			
	Steep rocky ridge	Moderate rocky hillside	Edge of valley floor	Totals
Vertical clefts in low cliff	1			1
Ledges and crevices in sandstone outcrop		3		3
Loose rock slabs and boulders		2	1	3
Big rock blocks		1	1	2
Totals	1	6	2	9

Dens studied near Mack and Loma were along a ridge of sedimentary rocks just north of the Colorado River and on the south side of the Grand Valley. The Uncompahgre Plateau south of the Grand Valley is a broad uplift capped by the Dakota formation and terminating to the northeast in a monocline that plunges beneath the floor of the Grand Valley. Through the northwestern end of this monocline, the Colorado River has cut a narrow canyon separating the plunging strata of the monocline, forming the ridge north of the river, from the plateau south of the river. The Dakota formation, a resistant Cretaceous sandstone, covers the northeastern slope of the ridge and has weathered out to form ledge outcrops along the northern and eastern slopes, and low cliffs facing southwest along the crest of the ridge. In these ledges and cliffs and under blocks fallen therefrom were found 7 of the 9 dens studied, and numerous others at which no rats were caught. (See Pl. 42, Figs. 1-3.)

Scattered Utah junipers grow on the north slope of the ridge. Near the east end in the vicinity of Loma grows another tall shrub, the singleleaf ash.

Among the numerous low shrubs that dot the stony soil are shadscale, snakeweed, *Ephedra*, sagebrush, and Russian thistle. A thick stand of greasewood in the bottom of a sandy wash cutting through the ridge southwest of Mack was unoccupied by wood rats though rats were numerous on the adjoining rocky hillside.

A few desert wood rat dens were found on the West Fork of Douglas Creek south of Rangely. The valley was U-shaped with a flat bottom fringed with alluvial fans and talus from the bordering canyon walls and rimrock. At the foot of the talus slope there were scattered large sandstone blocks that had fallen from the nearly horizontal strata of the Williams Fork formation forming the western rim of the valley. The rat dens were under the largest of these blocks. The valley floor was covered with tall greasewood among which no dens could be found. Along the gently sloping western side of the valley floor the vegetation was mainly short grasses, scattered low shrubs (shadscale, *Atriplex nuttallii*, sagebrush), Russian thistle, and numerous clumps of hunger cactus. In this belt the greasewood thinned out and reached its upper limit. On the steep rocky talus slope grew scattered Utah junipers. Desert wood rats probably lived under large rocks higher up the talus slope, possibly even along the rim of the cliff, but no search was made there.

DENS

Although houses built by the desert wood rat have been reported by Cary (see p. 519), I have obtained this species only at rock dens. From the great scarcity of wood rat houses of any kind in northwestern Colorado I conclude that rock dens are the more typical type of shelter for *N. l. sanrafaeli*. In general, the material accumulated by *lepida* at its dens contains more slender sticks and fewer bones than that collected by *cinerea*, but the wide range of variation makes it difficult to recognize the dens as those of *lepida* unless the occupant is caught or seen. The proportion of cactus spines in the midden is less than in middens of *albigula* but perhaps more than in middens of *cinerea*.

Some dens on the ridge south of Mack and Loma were in smaller crevices than I have seen utilized by other species of wood rats. Most of these crevices were horizontal or diagonal, and some were narrow spaces under relatively small rock slabs. Food litter and other debris were seen in crevices only one and one-half inches wide. Many rock clefts and den accumulations seen, however, were as large as those of most *Neotoma cinerea* in Colorado. At all localities where desert wood rats were caught, many more dens were seen in horizontal or diagonal crevices than in nearly vertical rock clefts, and nearly all were on the ground level. Most of the vertical crevices seen on the ridge southwest of Mack were unoccupied. On the ridge south of Loma, one *N. l. sanrafaeli* was caught at a den in nearly vertical clefts, described below. This was the only den studied at a site closely resembling that usually preferred by *N. cinerea.* Considering the types of den construction, the other dens most resembled those of *N. albigula,* and to a lesser extent those of *N. mexicana.*

Materials accumulated at dens, and the number of dens at which each occurred are as follows: sticks, 9 (shadscale 3, juniper 2, sagebrush 2, singleleaf ash 2); bones, 7; prickly pear joints, 2; branches of Russian thistle, 1; cow dung, 1; cow hoof, 1; sandstone flakes, 1; fingers of old work-glove, 1. The largest item was a stick 19 inches long and 1½ inches in greatest diameter.

Nests or nesting materials were found at 5 of the 9 dens studied. Three of these were ball-shaped or shapeless masses of nesting materials with no clearly ascertainable cavity. They may have been collapsed abandoned nests, or the cavities may have been damaged in removal from the den. One of the other two nests was cup-shaped and the second was semicup-shaped or semidomed, as described on page 519 (den 491110-3). Nests were made of varying materials, fine dry grass being most abundantly used. One nest was made entirely of shredded juniper bark, and another was made of fine textured cuttings of snakeweed (*Gutierrezia*). Small amounts of shredded sage bark and fine food-litter were used in other nests.

The few nests found of *Neotoma lepida* were not appreciably smaller than most of the nests of *N. cinerea,* in spite of the considerably smaller size of *lepida.* The presence of fine food-litter in nesting material of the desert wood rat suggests that *N. lepida sanrafaeli* is not so particular about its choice of nesting materials as is *N. cinerea orolestes,* which, in the dens studied, nearly always used nothing but juniper or sage bark if these were available. Juniper bark was available at 7 of the 9 dens and sagebrush at 5 of the 9 dens of *N. lepida.* Grasses and snakeweed may have been used by *lepida* because of their abundance close at hand.

An example of a fairly typical den of the desert wood rat in Colorado is one found on a rocky hillside one mile southwest of Mack at 4600 feet elevation. A young adult female (480908-5) was trapped there on 8 September 1948. The habitat is described on page 515. On the hillside, which slopes towards the north, there is a series of sandstone outcrops in lines running up and down the slope. The den had a western exposure, under loose blocks and pieces of sandstone that had weathered out and fallen from the edge of such an outcrop. The principal shelter was a rock slab about 10 feet long and 1 to 3 feet thick. The den was in good fresh condition when examined.

A space roughly seven feet long, under one side of the rock slab that formed the roof, was nearly filled with sticks and cuttings. Inside the entrance on the lower side of the den the stick pile was cemented together with a brown fecal deposit. The den materials brought in by the wood rat consisted mostly of sticks of shadcale, with some sticks and bark of Utah juniper. There were a few sheep or deer bones and some cactus spines (*Opuntia*). The food litter consisted mostly of cuttings and twigs of Utah juniper and shadscale. The spiny areoles of *Opuntia* must also be considered food litter. There was a cup-shaped mass of fine dry herbaceous cuttings of snakeweed resting on sticks and food litter high under the middle of the slab roof. The shape and texture of this mass indicated that it was a nest.

A den in tidy condition with a deep vertical crevice and excellent drainage, was in the low southwest-facing cliff on the ridge one and a half miles southwest of Loma. The den crevices were between and behind blocks of standstone that had broken loose from the standing rock but remained in place (see Pl. 44, Fig. 2). The shelter situation, particularly the main vertical cleft, looked to be adequate for *N. cinerea arizonae,* which occurs in the same area. However, I trapped a young adult male *N. lepida sanrafaeli* (491107-3) at this den on 7 November 1949.

In the main vertical cleft between the largest block and the bedrock there was a consolidated fecal midden on which lay food litter consisting mostly of fresh cuttings of *Eriogonum* and old cuttings of shadscale, with sections of yucca leaves and a few old twigs of singleleaf ash. Accumulated den material other than the food litter was scarce—only a few small sticks of ash, the humerus of a cottontail, and a few dry leaves, probably windblown. There were small fecal deposits in cracks of the weathered diagonal bedding plane above the main block and main vertical cleft.

An unusual den was found on the West Fork of Douglas Creek, 2 miles east and 18 miles south of Rangely, at 6200 feet elevation. It had one of the largest middens I have seen at any wood rat den. An adult female (491110-3) was trapped there on 10 November 1949. The habitat is described on page 516.

The den was under two huge sandstone blocks, the larger of which was leaning against the side of the smaller and had broken into two parts separated by a narrow vertical cleft. The originally larger single block was approximately 30 feet long and 9 feet high. Underneath and between the blocks was a cavelike "room" with a sloping roof and two entrances, one big enough for a man to walk into and the other, at the opposite end, only 3 or 4 feet high. The "room" was estimated to be 25 feet long and 6 feet high. Immediately inside the smaller entrance to the cavelike room and underneath the low rock overhang was an old dry skeleton of a cow with dry hide still covering most of the bones. Dry rat pellets littered the floor of the room and the ground inside the rib basket of the skeleton.

Along each side of the "room" there was a big wood rat midden. The one on the west side was the smaller (about six feet long) and adjoined the cleft through the large leaning sandstone block. The midden along the east side lay on a low rock shelf and measured 12 feet long, from 3 to 4 feet wide along most of its length, and up to a maximum of 1 foot deep. Its volume was estimated at 25 cubic feet. Behind the midden pile the den extended underneath the large block. I do not know whether the two middens belonged to separate dens occupied by two wood rats or whether they were separate portions of the same den occupied by a single rat. (See Pl. 44, Fig. 3.)

The midden material consisted almost entirely of a mixture of sticks, dry cow dung, bones, dry Russian thistle, dry joints and spines of *Opuntia polyacantha,* and large quantities of wood rat feces. The material was loose, mixed, and dusty, with most of the sticks and Russian thistle lying on the surface. The sticks on the two middens were mostly smaller than sticks usually seen at dens of *N. cinerea.* The midden material might have passed for that of *N. albigula brevicauda* except that the proportion of cactus spines was considerably less—not enough to form a solid bed of areoles. Food litter found on the two middens consisted of cuttings of Russian thistle, shadscale, *Atriplex nuttallii,* greasewood, and *Lepidium montanum;* spine areoles of prickly pear; and a few cuttings of Utah juniper that must have been brought from at least 50 yards away.

Upon excavating the smaller midden from under the inclined base of the leaning rock I found a nest on the rear of the midden, abutting against the inclined rock ceiling. The front of the nest was open on top, but the nesting material, mostly dry grass and fine food litter, covered the back side against the rock. Before the den was disturbed, loose den material had been piled around the nest concealing it from view.

Houses 2 to 3 feet high, constructed of dried cow manure and the joints of prickly pear (*Opuntia* sp.), were reported by Cary (1911: 118-119), who found them on the first bench south of the White River, five miles west of Rangely, at 5300 feet elevation. He caught four rats of this species at entrances to the houses. The larger houses were in thickets of shadscale and the smaller houses in clumps of *Opuntia.* On 9 November 1949, I hunted for wood rat houses for an hour between 3 miles and 6½ miles west of Rangely on the shadscale flats, and for a shorter time among the greasewood bushes on the bottom land. I saw no sign of any houses such as were described by Cary, although rock dens of *Neotoma* were seen 6 miles west and 1½ miles south of Rangely. Traps set at these dens caught no rats. Perhaps houses are constructed on the flats by this species only at times of high population when all suitable rock shelters are occupied.

FOOD AND STORAGE

Most of the plants eaten by the desert wood rat are xerophitic shrubs, forbs, cacti, or shrubby trees. Foliage comprises the bulk of the food, with smaller amounts of the succulent joints of cacti. Occasionally stems, twigs, tender bark, seeds, or berries are eaten. Food litter remaining in and about the dens is composed mainly of twigs, partly eaten leaves and foliage cuttings, stems of forbs, and the spiny areoles of *Opuntia* cactus from which the succulent flesh has been eaten.

Russian thistle, *Atriplex,* and Utah juniper are much used as food by *N. l. sanrafaeli* and are widely available throughout its range in Colorado. These kinds of plants, however, may have little importance in the diet of the desert wood rat in distant parts of its range outside of Colorado, where other kinds of plants are available. Use of the Russian thistle, an introduced weed, is evidence that this wood rat is adaptable and opportunisitic in food habits. Cactus is eaten frequently but not in large amounts.

The desert wood rat is well adapted to subsistence in arid regions by its preference for xerophytic plants, but it is less specialized for desert life than the white-throated wood rat. Although all species of wood rats in western Colorado eat shadscale and Russian thistle, these plants rate higher on the preference list of *N. l. sanrafaeli* than they do on the list of any other kind of wood rat. *N. lepida* is intermediate between *N. albigula* and *N. cincerea* in quantity of cactus consumed and is less dependent upon it than is *albigula.*

Information concerning food is presented in the following paragraphs for each of nine dens examined. For explanation of the arrangement of plant names and the use of symbols see page 380.

One Mile Southwest of Mack, 4600 Feet

8 September 1949.—480908-1. ++ *Salsola kali,* - *Gutierrezia sarothrae; Rhus trilobata, Atriplex confertifolia.* There was little, if any, sign of pruning on the clump of skunkbush.

480908-2 & 3. * *Atriplex confertifolia,* * *Salsola kali; Gutierrezia sarothrae, Juniperus utahensis.* None of the food litter was fresh.

480908-5. + *Juniperus utahensis,* + *Atriplex confertifolia,* * *Gutierrezia sarothrae,* * *Salsola kali,* - *Opuntia polyacantha; Ephedra viridis.*

480908-7. + *Juniperus utahensis,* + *Atriplex confertifolia,* - *Salsola kali; Ephedra viridis.* There was a layer of juniper needles and shadscale twigs 1 to 10 inches deep. No juniper berries or seeds were seen on the midden.

480908-8. + *Salsola kali,* * *Atriplex confertifolia,* - *Mirabilis linearis,* - *Artemisia tridentata,* - *Gutierrezia sarothrae,* - *Opuntia polyacantha. Mirabilis linearis* growing close to the den was slightly pruned. The only cuttings of sagebrush and snakeweed were a few flower clusters.

In some places there were small accumulations of juniper berries and bare nutlets on ledges near dens of *Neotoma,* but the indications were that these accumulations resulted from the work of chipmunks *(Eutamias)* or white-footed mice (*Peromyscus*). (See p. 467.) Such accumulations were found away from the immediate entrances of dens and in places where rat pellets were scarce.

One and One-half Mile South of Loma, 4600 Feet

7 November 1949.—491107-3. + *Eriogonum* sp., + *Atriplex confertifolia,* * *Yucca angustissima,* - *Fraxinus anomala,* -- *Juniperus utahensis,* -- unidentified Cruciferae; *Gutierrezia* sp., *Amelanchier utahensis, Artemisia tridentata, Cirsium* sp., *Ephedra viridis, Brickellia* sp. The remains of buckwheat consisted almost entirely of cuttings of flower clusters.

491107-2. * *Fraxinus anomala,* * *Yucca angustissima,* * *Atriplex confertifolia,* * *Streptanthus cordatus,* - *Gutierrezia* sp., - *Juniperus utahensis,* - *Eriogonum* sp. -- *Opuntia rhodantha; Artemisia tridentata, Chrysothamnus greenei, Amelanchier utahensis, Chrysopsis* sp. The litter from the singleleaf ash consisted of leaves, twigs, and samaras. Seeds had been removed from some of the samaras. The remains of *Streptanthus* consisted of dry stalks and capsules. The nearest cactus grew more than 100 feet from the den.

Two Miles East and Eighteeen Miles South of Rangely, 6200 Feet

10 November 1949.—491110-2. * *Salsola kali,* * *Atriplex confertifolia,* * *Sarcobatus vermiculatus,* * *Atriplex nuttallii,* **Lepidium montanum,* - *Artemisia tridentata,* - *Opuntia polyacantha,* -- *Juniperus utahensis,* -- *Bouteloua* sp. The nearest juniper grew more than 100 feet from the den.

491110-3. * *Salsola kali,* * *Opuntia polyacantha,* * *Atriplex confertifolia,* * *Atriplex nuttallii,* * *Lepidium montanum,* * *Sarcobatus vermiculatus,* -*Juniperus utahensis,* - *Bouteloua* sp.; *Artemisia tridentata.* The nearest juniper and sagebrush were growing more than 50 yards from the den.

A summary of food data obtained at nine dens of *N. l. sanrafaeli* is presented in Table 35 in order to show the relative preference for each kind of food plant. A high relative preference is indicated by the high percentage of dens at which the available plant was eaten. The quantities of each plant in the food litter and the proximities of the available plants also were considered in arranging the plants roughly in order of decreasing preference. Only a few kinds of plants, however, have been recorded frequently enough to lend significance to the figures on preference.

TABLE 35.—PLANTS AVAILABLE AND USED AS FOOD AT 9 DENS OF N. L. SANRAFELI (PLANTS LISTED ROUGHLY IN ORDER OF RELATIVE PREFERENCE)

PLANTS	Number of dens at which plant occurred		
	within 100 feet	as food litter	as stored food
Salsola kali	7	7 (100%)	1
Juniperus utahensis	5	6 (120%)	
Atriplex confertifolia	9	8 (89%)	
Atriplex nuttallii	2	2 (100%)	
Fraxinus anomala	2	2 (100%)	1
Opuntia	4	5 (120%)	
Eriogonum	2	2 (100%)	
Sarcobatus vermiculatus	2	2 (100%)	
Yucca angustissima	2	2 (100%)	
Lepidium montanum	2	2 (100%)	
Bouteloua	2	2 (100%)	
Streptanthus cordatus	1	1 (100%)	
Mirabilis linearis	1	1 (100%)	
Gutierrezia	6	4 (67%)	
Artemisia tridentata	3	1 (33%)	
Brickellia scabra	1		
Cirsium	1		
Chrysopsis	1		
Chrysothamnus greenei	1		
Rhus trilobata	1		
Amelanchier utahensis	2		
Ephedra viridis	3		

Only three of the nine dens studied had uneaten plant-cuttings in a quantity sufficient to warrant considering the food as stored. Den 480908-8 contained more than a gallon of dry cuttings of Russian thistle crammed back under a slab of rock. Den 491107-2 had leaves and fruits of singleleaf ash mixed through the sticks under the sheltering rock. Den 491110-2 had more than a quart of mixed cuttings with some food litter stuffed under a rock. At a fourth den (491110-3) uneaten mixed plant cuttings were scattered on the rear of the midden, but these were probably only a temporary food-store for daily feeding, such as was described for *N. fuscipes annectens* by Vestal (1938: 29).

REPRODUCTION AND YOUNG

Warren (1926: 99) reported collecting a female with five large embryos on 24 April and two immatures on 25 April 1912 at Mack, 4543 feet. Measurements of the immature male and female are, respectively: total length, 198, 200; tail vertebrae 78, 80; hind foot 29, 29; ear 26, 25. A subadult female (CM 9421) from Willow Creek, 5300 feet elevation, 16 miles south of Ouray, Uintah County, Utah, contained two embryos 40 mm long on 28 June 1933. She was in advanced postjuvenal molt and was probably not more than four months old. Her external measurements were 278-120-28-28. None of five females collected by me in September and November was pregnant or lactating.

The above records indicate that the young are born in early spring and in early summer and that there may be more than one litter per year. Females born early in the spring reach maturity before the close of the same breeding season. W. H. Burt (1934: 418) reported that specimens of *N. l. lepida* in southern Nevada bore four young per litter and at least two litters per year. Similar data have been reported for the same subspecies in the Providence Mountains area, California, by Johnson, Bryant, and Miller (1948: 369).

MOLTS

The patterns and progress of molts in *N. lepida* do not differ appreciably from those seen in *N. cinerea* (see p. 398). The seasonal distribution of specimens in molt is shown in Plate 22.

The juvenal molt is clearly illustrated by a subadult male (CM 9409) from 15 miles southwest of Ouray, Utah, 29 May 1933. Distinct longitudinal molt lines separate the ash gray juvenal pelage of the head, back, and rump from the light buff subadult pelage covering the sides, forelegs, and hips.

Simultaneous occurrence of the postjuvenal and second molts can be seen in CM 9420, first year adult male, from 16 miles south of Ouray, Utah, 28 June 1933. Most of the upper parts are in subadult pelage, but juvenal pelage remains on the crown and nape. Molt was in progress on the nape and between the eyes but had not yet converged onto the crown. The second molt is concealed along the lateral lines and sides of the hind legs, across the breast, and in front of the inguinal region. The first autumn pelage is full grown on the midabdomen. A young female (CM 9421) taken on the same day at the same place has the postjuvenal molt less advanced than on CM 9420, with the juvenal pelage extending from the head to the middle of the back. Inspection of the lower sides and venter revealed no trace of the second molt beginning.

Conclusive evidence of a third molt in *lepida* is demonstrated by BSC 148012, male, from five miles west of Rangely, 15 September 1906, which is a fine example of a first year adult with two molts in progress, one following closely after the other. There is no superficial sign of molt, the rat appearing to be in bright adult pelage, moderately worn on the nape. Ruffing of the fur reveals that the oldest pelage extends from the crown back over the nape and back in a roughly V-shaped pattern with the point ending in front of the rump. Under most of this pelage on the back, newer hairs had started to grow. Laterally and posteriorly the hairs of the newer pelage are full length covering the upper parts outside of the V-shaped area. The color and texture of the pelage within the V are so typically mature, that this pelage cannot be interpreted as juvenal, but must be subadult, in which case the molt replacing it is the second molt and the pelage on the sides and rump is the first autumn pelage. A later molt, the third of the year, is well under way along the lateral line and over the belly. The later pelage following the third molt is the first winter pelage, which has reached full length over nearly all of the abdomen but stops abruptly in front of the inguinal region. A line of the second molt extends along the lower side of the face.

An early stage of the annual molt can be seen on an old adult female (BSC 148015) from five miles west of Rangely, 16 September. The new pelage has grown out to full length on most of the abdomen, and there is a separate patch of molt on each side of the rump. Annual molt is well advanced on a second year adult female (DM 3972) from Cisco, Utah, 9 August 1940. The pelage is rough in appearance and the back and sides are molting heavily in patches. Richly colored new pelage is visible on the thighs, right lower side, and upper forelegs.

PARASITES

The kinds of parasites collected from desert wood rats in the present study and the field numbers of individual hosts are listed below.

Neotoma lepida sanrafaeli:

Laelaptidae

Brevisterna utahensis, 480908-2, 491107-2

Trombiculidae

Euschöngastia criceticola, 491107-2
Euschöngastia finleyi, 491107-3
Trombicula hoplai, 480908-1, 2, 3, 7 & 8
Trombicula potosina, 480908-1, 2, 3, 7 & 8

Hectopsyllidae

Echidnophaga gallinacea, 480908-1, 491107-3

Hystrichopsyllidae

Hystrichopsylla sp., 491110-3

Ceratophyllidae

Malaraeus sp., 491110-3
Orchopeas sexdentatus, 491107-2

COMPETITION AND ECOLOGIC DIVERGENCE

Wood rats of more than one species occur at the same localities in several parts of Colorado, as indicated in Figure 8. Such localities provide especially favorable opportunities for studying the ecologic relationships between sympatric kinds of wood rats. In many areas two species, and in some areas three, inhabit the same or adjacent habitats. The degree of competition between these coexisting species seems to be inversely related to the degree of ecologic divergence that has been attained.

In a recent review of the problem of interspecific competition (Crombie, 1947: 66), competition was well defined as "demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply." Wood rats present numerous examples of demand on the same resources, such as for food plants, nesting materials, and construction materials of the house. But in most of such instances, even when the population of wood rats is high, the immediate supply is more than ample for the population of all kinds of wood rats; hence competition for that resource does not exist. Suitable den shelter is the environmental resource most frequently fully exploited, hence most often limiting. Sites adequate for dens are seldom spaced closely enough together to house a population as large as could be supported by the supplies of food and other materials available. Under such conditions competition for den sites may be expected to exist between two or more kinds of wood rats to the extent that each requires the same kind of den shelter.

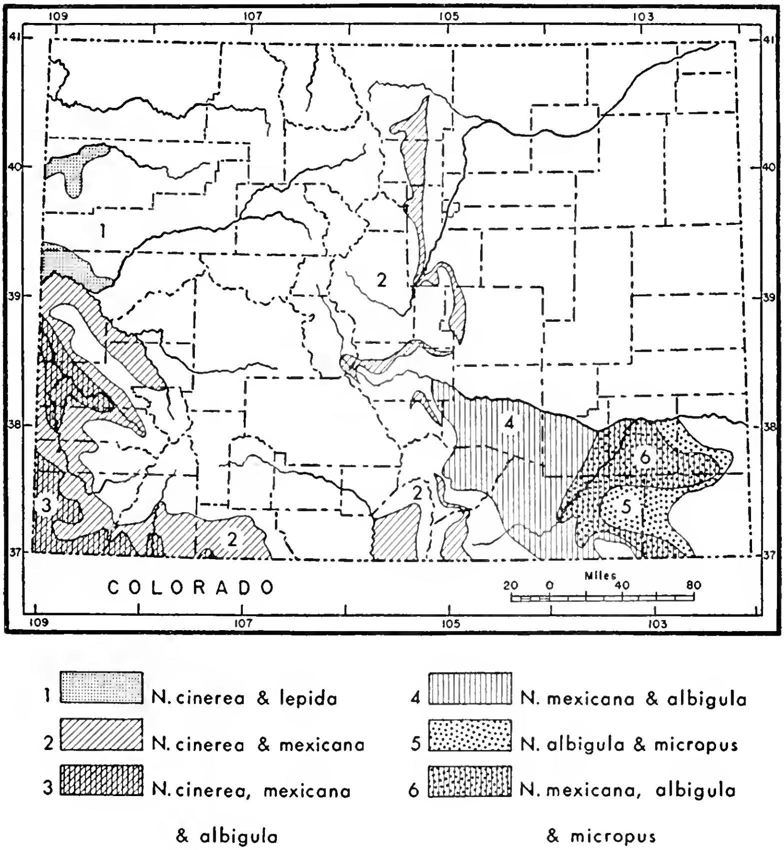


FIG. 8. Areas in which more than one species of wood rats probably occur at the same localities.

According to the thesis of Gause (1934: 19, 48, 113) based on mathematical considerations and laboratory population studies, two species having identical ecological requirements, that is to say, occupying the same ecological niche, cannot persist together in the same area. Competition for living space and resources of the environment would result in one species displacing the other. Evidence from study of the wood rats of Colorado supports this thesis.

I know of no area where two kinds of wood rats occupy only the same ecological niche. However, the complexities of mammalian life histories do not lend themselves to simple confirmation or contradiction of any ecological generalization. Environmental responses and coactions vary widely at different times and places under changing physical and biotic conditions. Competition between sympatric species of wood rats is avoided or reduced by ecological divergence, primarily in kinds of dens, and secondarily in food preferences. At some places the divergence results in local habitat separation, and at other places selection of different resources is made in the same habitat. These are in most cases matters of degree, and complete ecological separation probably seldom occurs.

Before reviewing the competitive position of each kind of wood rat relative to coexisting species in Colorado, it may be desirable to present a summary statement of the ecological niche of each species, with particular attention to niche differences. In the discussion that follows, no consideration is given to competition with animals other than wood rats. The influence of competition and ecologic divergence on geographic distribution will be considered in the following section.

N. cinerea thrives in the high mountainous parts of the state where it endures a climate with colder and longer winters than are experienced by any other kind of wood rat. It lives primarily in high cliffs or caves, or equivalent man-made habitats, to which it is well adapted by agility in climbing and its bushy tail. Its dens are usually in deep vertical crevices. Although large piles of sticks and bones are often built up around such a crevice, *N. cinerea* rarely builds a stick house where a sheltering crevice is not already present. At lower elevations subspecies of *N. cinerea* are less restricted to cliffs and vertical crevices but rarely inhabit level open country away from rocks. The food plants acceptable to *cinerea* are sufficiently varied and abundant to exclude them as limiting factors either by absence of food or competition with other wood rats for the same food.

N. mexicana inhabits the eastern foothills of the Rockies and the canyon country of western Colorado. It does not occur higher than the Transition Life-zone. Its dens are rarely situated away from rocks, but the kinds of rock shelters used are more varied than in the case of *N. cinerea*. The collecting instinct seems less strongly developed in *N. mexicana* than in any of the other wood rats, and stick houses are not built away from rocks. Food plants acceptable to *mexicana* are almost as varied as for *cinerea,* but cacti are eaten only in extremely small amounts, and soft-leaved plants are much preferred over sclerophyll and xerophytic ones.

N. albigula is confined to low elevations in the southwestern and southeastern corners of the state. It is specialized for life in desert and semidesert regions, which have only limited extent in Colorado. The most preferred foods of *albigula* are cactus joints and, secondly, juniper needles. The importance of cactus in the life of *albigula* is also evident from the abundance of joints and spines utilized in building the dens. These may be either among rocks or in the open where houses of cactus joints, sticks, and cow dung are built around the base of a bush or clump of cactus. When *N. albigula* lives among rocks it prefers horizontal to vertical clefts and does not climb high cliffs as readily as *cinerea* and *mexicana.* But *albigula* has amazing agility in scampering among the branches of cholla cactus without being injured by the spines.

N. micropus is a rat of the hot semiarid country in the southeast corner of Colorado and has adaptations similar to those of *N. albigula. N. micropus* depends heavily upon cactus for food and shelter when these are available. Its dens may be among rocks or, more usually, may be stick or cactus houses away from rocks. No distinctions could be recognized between the food and shelter requirements of *micropus* and those of *albigula.* These species seem to come into competition wherever they meet in southeastern Colorado. However, such competition usually results in the restriction of *albigula* to habitats where natural rock shelters are at hand and the restriction of *micropus* to more level terrain where no rocks are available and houses are constructed.

N. floridana is the wood rat of the High Plains and ranges westward up the Arkansas Valley as far as the foothills. Its denning habits resemble those of *albigula* and *micropus* in ability to make use of rock shelters or construct houses away from the rocks. However *floridana* is much less partial to cactus joints as den material and as food. Where tree cacti are available, *floridana* frequently builds houses in them, but such houses usually are composed of less cactus and more sticks, stalks, and cow dung than those of *albigula* or *micropus.* In Yuma County, which is outside of the range of the tree cactus, *floridana* lives under the low rock outcrops forming the rims of gulches and feeds on yucca and the leaves of shrubs and forbs. Here its habits resemble those of *mexicana* in the foothill zone. In general the habits and requirements of *floridana* are intermediate between those of *micropus* and *mexicana*, but more like those of the former.

N. lepida has such a restricted range in western Colorado that no clear picture of its particular ecological niche was obtained in the course of this study. Its food and den characteristics in western Colorado are much like those of *albigula*, from which it is separated by the Colorado River. Its dens are usually in rock crevices or under boulders, and considerable amounts of cactus are sometimes gathered for shelter and food. The smaller size of *lepida* enables it to occupy slightly smaller crevices and rock shelters than *albigula*.

Throughout most of its range *N. cinerea* does not come in contact with any other kind of wood rat. On the eastern fringes of its range the lower limit of *N. c. orolestes* overlaps the upper limit of *N. mexicana fallax*. Cary (1911: 117) reported this zone of overlap west of Boulder to extend from 5800 feet to approximately 7500 feet. In this zone it is unlikely that *orolestes* and *fallax* compete for food, in spite of their similar preferences, because food is abundant and could support much larger populations of both kinds of rats than are able to find adequate shelter. There is probably some competition for favorable den sites, for the larger vertical rock crevices, caves and buildings are satisfactory for *fallax* as well as *orolestes*. Competition for shelter is probably partly relieved by the preference of *orolestes* for high vertical crevices, and *fallax* for lower crevices and boulders, thus preventing one species from driving the other out of the zone of overlap.

The ecological relations of *N. c. orolestes* with *N. m. scopulorum* and *N. albigula warreni* on the eastern flank of the Sangre de Cristo Mountains are still unknown. To the best of my knowledge (based on inadequate collecting) *orolestes* does not occur below the Transition Life-zone. Probably *orolestes* competes for den sites with *scopulorum* in the Transition Life-zone but does not reach the lower elevations where *N. a warreni* occurs.

In southwestern Colorado *N. cinerea arizonae* occupies the same area covered by *N. mexicana inopinata*, and occurs also at higher elevations where these exist. At numerous localities, such as those west of Cahone, in McElmo Canyon west of Cortez, and on Mesa Verde, *arizonae* and *inopinata* were taken in the same rocky habitats. No clear distinction could be recognized between the types of rock shelters chosen by these two forms but *arizonae* usually occupied the higher vertical clefts or the larger fallen blocks. Such a distinction broke down frequently enough to justify the conclusion that these two species compete for den sites in at least some situations. One mile east of Naturita, at 5900 feet elevation, I caught only *mexicana* in a cave and high vertical crevices of a cliff where I fully expected to find *cinerea,* none of which was obtained at that locality. Perhaps if *cinerea* had been present it would have occupied the cliff site and driven *mexicana* to lower and smaller rock shelters. There was no dirth of food for both species in western Colorado and little difference in preference. *N. cinerea* ate a larger proportion of piñon needles when available and relatively less of juniper.

The dens of *N. cinerea* could often be distinguished from those of *N. mexicana* in eastern as well as western Colorado by the greater amounts of large sticks, bones, and cactus joints accumulated by *cinerea.* But there were conspicuous exceptions.

The clearest habitat distinctions between wood rats were observed in Dolores Canyon near Gateway. The Mexican wood rat was trapped on the steep lower canyon sides and at the bases of cliffs near the valley bottom. The white-throated wood rat was trapped on the valley floor of John Brown Creek, on boulder-strewn alluvial fans and benches, and along the edges of the benches and bottomland at the bases of cliffs and steep slopes. Only in the latter situations does *N. albigula brevicauda* encounter *N. mexicana inopinata,* both of which occupy low rock crevices and spaces beneath sandstone blocks. *N. mexicana* does not occur away from rock shelters and builds no stick houses, but *albigula* builds numerous large houses of sticks, dung, and cactus joints on the alluvial gravels away from large rock shelters, usually using a clump of cactus, juniper, or sagebrush as a base. Where both species occur along the base of a cliff, the dens of *albigula* are instantly recognizable by their immense quantities of cactus spines, which are almost totally absent from the dens of *mexicana.* Perhaps these two species compete for den sites among rocks but it seems likely that such competition is slight because of the different kinds and quantities of materials gathered for utilization of such sites. A den once used by *albigula* must surely convey some advantage to succeeding generations of that species. Farther up the canyon sides where cactus is scarce and rock shelters numerous, only *mexicana* occurs. The marked differences in food preferences between the species and the abundance of food plants eliminates any possibility of competition for food.

N. cinerea also occurs in Dolores Canyon near Gateway, but seemingly only at higher elevations in the cliffs. Mr. Lyman Hubbard, of Gateway, who was aware of the distinction between bushy-tailed and round-tailed wood rats, informed me that he did not recall ever seeing bushy-tailed wood rats below the upper part of the Wingate sandstone, which is the lowest of the sheer cliff-forming rocks of Dolores Canyon. He said they occur in cliffs and mine tunnels anywhere on up from the Wingate through the Entrada, Morrison, and Dakota formations and above the canyon rim in the "cedars" (*Juniperus utahensis*) on the flanks of the La Sal Mountains. Although I trapped no specimens of *cinerea,* I observed that none of the rocks below the Wingate have many large deep vertical crevices. *N. cinerea* probably encounters *mexicana* somewhere near the base of the Wingate sandstone at an elevation between 5500 and 6000 feet. Possibly *cinerea* is absent at lower levels as a result of competition for shelter, which favors *mexicana* below the Wingate and *cinerea* above.

The Mexican and the white-throated wood rats live in the same habitats at many localities in southwestern Colorado. At Bondad a male *N. m. inopinata* and a male *N. a. laplataensis* were trapped on the same night at separate entrances of the same den (490615-5). It was evident from the scarcity of cactus spines in the midden that the den belonged to *mexicana.* Other dens with middens characteristic of either *mexicana* or *albigula* were numerous among rocks of the same rim outcrop. Under a large sandstone block a mile east of Naturita there was an occupied den of *N. mexicana* (490626-4) and an unoccupied den of *N. albigula,* each with its own distinct midden separated by only two and a half feet. In Dolores Canyon north of Egnar dens of both species were seen but the population of *albigula* seemed to be low or perhaps had been wiped out; two dens of this species had only recently been taken over by *mexicana.* At none of these localities was there any evidence of *albigula* building houses out away from rock shelter, such as enabled *albigula* to occupy a habitat separate from *mexicana* in Dolores Canyon near Gateway. Since habitat separation between *mexicana* and *albigula* in most parts of southwestern Colorado is slight, and choice of den situations is so similar, there is probably some competition for shelter between these species, but only during times when the combined populations in a given area exceed the number of favorable den sites. Competition is probably to a considerable extent relieved by the ability of *mexicana* to occupy higher cliff crevices when available and the preference of *albigula* for dens with large quantities of cactus spines. The considerable differences in food preferences between these rats and the general excess of food available virtually eliminates any possibility of competition for food.

N. c. arizonae and *N. a. laplataensis* inhabit the same parts of southwestern Colorado and at some places even the same habitats. But competition between them, either for shelter or food, is probably slight. *N. albigula* uses vertical clefts even less than *mexicana* does. Although *cinerea* eats and accumulates more cactus than *mexicana,* it does not use more than a small fraction of the quantities used by *albigula.*

Although I did not obtain *N. cinerea* and *N. lepida* together at any locality, they probably do come in contact. The similarity of ecological niches occupied by *lepida* and *albigula* suggests that competition between *lepida* and *cinerea* is no greater than between *albigula* and *cinerea.* The small size of *lepida* would also help relieve it from competition for den crevices with any other kind of wood rat. Geographic separation of *lepida* from *albigula* by the Colorado River prevents any possibility of competition between these ecologically similar species.

The ecological relations between *N. mexicana* and *N. albigula* in eastern Colorado are basically the same as in western Colorado. Both species occur together along rock outcrops and low cliffs of canyons cutting through the High Plains; but *albigula* alone builds houses out on the flats, as it does in western Colorado near Gateway. Houses on the alluvial flanks of the Purgatoire Valley at Higbee were built around tree cactus and were composed of tree cactus joints and cow dung. The houses on the rolling upland surface of the High Plains north of Higbee usually were at the bases of junipers and were composed mostly of cow dung and juniper sticks and twigs. There may be slight competition between *albigula* and *mexicana* for den sites among rocks on the canyon sides. But there could hardly be any competition for food.

A third kind of wood rat, *N. micropus,* coexists in southeastern Colorado with *albigula* and *mexicana.* Its habits and requirements are almost the same as those of *albigula* and differ from those of *mexicana* in virtually the same respects. However, *micropus* is not always found at the same localities as *albigula,* and the denning habits as well as the habitat occurrence of each species seem to be influenced by the presence or absence of the other. At Higbee where no *micropus* were found in 1950, *albigula* occupied cactus houses, stick houses in junipers, and rock crevices and blocks. At

Monon in 1905 Warren (1942: 211) found *micropus,* in the absence of *albigula,* living among rock ledges and crevices bordering Bear Creek. Just over the line in Kansas, *micropus* was reported extremely numerous in the same situation in 1950 by Cockrum (1952: 190). Both these points are outside of the ranges of *albigula* and of the tree cactus. From my own examination of the terrain along Bear Creek it was evident that junipers were absent and prickly pear cacti were too scattered to provide clumps in which the rats could form houses. At the head of Chacuaco Creek, 11 miles north and 8 miles east of Branson, I collected both *albigula* and *micropus.* Only a single *albigula* was obtained, an adult from a den under a rock ledge at the rim of the little valley. An adult *micropus* was taken at a second entrance at the opposite end of the same ledge. Other *micropus* were obtained at tree-cactus houses on the valley floor and under a huge sandstone block at the foot of the slope. The few specimens obtained at this location suggest some competition for den sites, with lack of habitat separation. The only other kind of den seen probably belonged to *mexicana.* At Regnier and other localities in southwestern Baca County, both *micropus* and *albigula* were numerous in 1951, and a clear habitat separation between these species was evident. *N. micropus* was obtained only from tree cactus houses on the alluvial fans flanking the valley bottoms. *N. albigula* was obtained only among rocks on steeper slopes and from stick and cactus houses built around junipers either on the steep slopes or above the valley rim. A high proportion of sites that to me seemed adequate for den shelter did contain dens. Although the amount of acceptable food available did not compare with that available in the foothill and mountain zones, it seemed to be more than ample and within easy reach of all dens. The conclusion seems justified that in the area around Regnier *micropus* and *albigula* were in close competition for den sites and that this competition was responsible for the restriction of each species to a separate habitat conveying some selective advantage to the species using it. It is clear from the occurrences of these species elsewhere that both are capable of making the same kinds of dens in the same habitats, if permitted to do so. Under low population pressure when competition is reduced, both species may occupy the same habitats. But under high population pressure any slight divergence in shelter adaptations should lead to confinement of each species to situations in which it had some competitive advantage in utilization of the limited resources of the environment.

It is not clear what advantage *micropus* enjoys over *albigula* in clumps of tree cactus in the open, or what advantage *albigula* gains under the shelter of rocks. Possibly the slightly larger average size and relatively larger feet of *micropus* give it some advantage in open country in combat with *albigula* or in ability to construct more sturdy houses more secure against predators.

Since the sympatric distribution of *micropus* and *albigula* in Colorado represents only a small part of the total area over which these species overlap, understanding of the relationships in Arizona, New Mexico, Texas, and northern Mexico is necessary for a reliable interpretation of their ecological divergence and present status. Although field work in other states was beyond the scope of the present study, a few published reports shed light on the status of these wood rats.

Vernon Bailey wrote concerning *N. micropus* in New Mexico, "It occupies mainly Lower Sonoran valleys, and unlike most of the species of wood rats, its home is rarely associated with rocks or cliffs" (Bailey, 1931: 171). Concerning *N. albigula* in New Mexico he wrote, "They show a strong preference for rough country and when possible choose rocks and cliffs for their homes" (*op. cit.:* 175). At Clayton in northeastern New Mexico A. H. Howell collected three specimens of *albigula* in a rocky pasture near town (*op. cit.:* 181). "At Santa Rosa . . . [*micropus*] were fairly common, usually living in houses built among the cactus and often close to cliffs occupied by *albigula*" (*op. cit.:* 172). A similar situation was reported near Cuervo, about 20 miles east of Santa Rosa. Several collectors found *micropus* abundant in the Pecos Valley living in stick, thorn, and rubbish houses under cactus and thorny bushes, "but they were not found reaching into the foothills of the mountains where the white-throated wood rat occupied the cliffs and rocky situations" (*loc. cit.*). In the Rio Grande Valley the situation is less clear. Houses built in the characteristic fashion of *micropus* were common along the sides of the valley and out over the mesas east of Mesilla Park and west of San Marcial, and a few specimens were taken, some of which were at entrances to burrows under prickly pears or clumps of grass. Ten miles northeast of Socorro *albigula* was reported living in the rocks not far from where *micropus* was living in burrows (*op. cit.:* 173). But other houses in the Rio Grande Valley, placed in dense clusters of saltbush, small-leafed sumac (*Rhus microphylla*) and skunkbush (*Rhus trilobata*), were attributed to *albigula* (*op. cit.:* 177). Also in the San Andres Mountains, east of the Rio Grande Valley, a house "built mainly of dried horse manure, pieces of spiny cactus, and branches of ocotillo and allthorn, the spiniest shrubs of the region" was attributed to *albigula* (*op. cit.:* 176).

All localities mentioned in the above paragraph are within the known ranges of both *micropus* and *albigula,* although the species are often topographically separated as mentioned above. But what of the habitat selection and denning habits of *albigula* in Arizona, where *micropus* does not occur? There *albigula* is an abundant resident of the Lower Sonoran desert where it builds conspicuous houses of sticks, cactus joints, and dried dung under a wide variety of desert shrubs and cacti on the sandy mesas and alluvial bottom lands (Vorhies and Taylor, 1940). This wood rat also occasionally occupies holes and crevices in the banks of washes, and crevices in rocky hills. Vorhies and Taylor summarize a wealth of detailed observations in southern Arizona thus: "Familiarity with the Lower Sonoran wood rat territory gives a distinct impression that cactus of the genus *Opuntia* is a most important factor in determining the abundance of *albigula.* In those areas of the Santa Rita Experimental Range where cactus is most abundant wood rats are most plentiful, and they are distinctly less numerous where cactus is scarce" (*op. cit.:* 464). The same authors collected *albigula* from large conspicuous houses beneath junipers and piñon pines in the Upper Sonoran Life-zone south of Holbrook and Winslow. Goldman collected *albigula* from dens among loose rocks and sandstone ledges in the Grand Canyon (south side) between 3800 and 6500 feet elevation (*op. cit.:* 467). Dens in rock crevices, under boulders, and in clumps of cactus or brush in southern Arizona have also been reported by Burt (1933: 120) and Cahalane (1939: 434-435). Houses in a wide variety of situations and a few dens among rocks were reported in Arizona and northern Sonora by Mearns (1907: 477-480).

In western New Mexico, west of the Rio Grande Valley and the plains about Deming, *N. micropus* is absent or scarce, and the habitats and dens occupied by *N. albigula* seem not to differ greatly from those occupied in Arizona. On Cactus Flat, between the Gila and San Francisco rivers, *albigula* built large houses of cactus joints and cow chips under bunches of bush cactus (*Opuntia schottii*). At Glenwood on the San Francisco River *albigula* lived in houses of cow chips, sticks, bones and other rubbish on the brushy banks of gulches. At Gallup and San Rafael in northwestern New Mexico and in the Chama Valley near Abiquiu, *albigula* lived in houses about the bases of junipers and tree cactus, and in rock crevices of lava beds and limestone cliffs (Bailey, 1931: 176-177).

From the foregoing reports it is evident that the western limit of *micropus* coincides roughly with a significant change in the habitat selection and denning habits of *albigula*. East of this limit *albigula* lives in rocky habitats, but seldom on open desert flats. West of this line *albigula* lives primarily on the open desert flats but also among rocks in certain places. Bailey described the situation at Deming in the following words: "Near Deming, in 1908, E. A. Goldman collected one specimen of . . . [*micropus*] in a brush patch near the sink of the Rio Mimbres, but in the same general region he found the white-throated species much commoner. From Deming westward the white-throated rat seemed to adopt the habit of . . . [*micropus*], living in houses built in the open valley. Many of these houses, however, were probably originally built by . . . [*micropus*] and later, when deserted, taken possession of by their white-throated neighbors" (*op. cit.*: 173). Whether *albigula* actually occupied dens deserted by *micropus* seems doubtful and would depend upon the fluctuations of population dynamics of these species on the Deming Plain. But the significance of the situation lies in the fact that at Deming *micropus* lives under marginal environmental conditions. For Deming is close to the western limit of the range of *micropus*. *N. albigula*, on the other hand, is abundant from Deming west through Arizona and is the characteristic wood rat of the desert plains and valleys. It seems likely that *albigula*, at least in favorable years, is able to build its own houses on the Deming plain and occupy them in successful competition with *micropus*.

In Texas both *micropus* and *albigula* range over much of the western half of the state. Vernon Bailey's survey of the state gives much useful information on the wood rats. Concerning *micropus*, "It lives mainly in the half open country and builds houses under mesquites, acacias, zizyphus, allthorn, or anything else sufficiently thorny to prove an effectual protection against its enemies. Rarely it lives among rocks" (Bailey, 1905: 111). Concerning *albigula*, "It apparently belongs to Upper Sonoran zone, but along cliffs and rocky gulches extends into the upper edge of Lower Sonoran, and so slightly overlaps the range of the larger and grayer *micropus* . . . but each retains its distinctive characters and habits, *micropus* living mainly in its stick houses in the brush, and *albigula* always keeping among the rocks along cliffs and gulches. In a few cases I have caught *micropus* in the rocks, but have never found *albigula* away from them" (*op. cit.:* 113-114).

N. micropus ranges considerably farther eastward than *albigula.* At Wichita Falls, beyond the range of *albigula,* abundant characteristic houses were attributed to *micropus* (*op. cit.:* 111). But at the northeastern limit of its range, in Barber County, Kansas, *micropus* was commonly found in caves and under rock ledges (Cockrum, verbal communication). Information at hand is insufficient to determine the reason for these differences in denning habits.

Along the Mexican border of Texas, *N. micropus* lives in woods, usually near water, often in the fringe of cottonwood and willow growth along rivers. Dens are made around the roots of decayed trees surrounded by thickets (Mearns, 1907: 471-472). But other reports indicate that it is by no means confined to these situations. In Aransas County, Texas, *micropus* builds stick houses under mesquite bushes (J. A. Allen, 1894: 165). In the Big Bend area *micropus* "was widely distributed from the river bottom up to 3500 feet elevation. Its houses, composed of sticks and pieces of cactus, were usually situated in mesquite, catclaw, or cactus, but a few were found in old dwellings and among rocks" (Borell and Bryant, 1942: 35). In the same area *N. albigula* was obtained in the Chisos Mountains between 5000 and 5200 feet at houses in or near *Agave lecheguilla* and in heavy brush (*op. cit.:* 36). These reports suggest an altitudinal separation in the Big Bend area possibly because of some climatic factor rather than competition. More detailed field studies in southern and western Texas and in northern Mexico would help greatly to clarify the relationships of these two species.

The reports reviewed above of habitats and dens of *N. micropus* and *N. albigula* in New Mexico, Arizona, and Texas reveal wide geographic variations that are consistent with my interpretation of the relationship between these two species in Colorado. Over much of their ranges these species seem to have basically similar ecologic requirements and to compete for den sites wherever they come together in sufficient numbers. Such competition is probably an important factor in the local distribution of both species. There are some indications that climatic factors may play a more important role in their separation in the southern parts of their ranges.

Ecological evidence supports the morphological evidence concerning the evolutionary relationship of *micropus* and *albigula.* They are closely related species difficult to distinguish in southeastern Colorado but morphologically more distinct and ecologically more divergent farther south. They seem to hybridize occasionally in Colorado (see pp. 302 to 308), but probably never do in southern New Mexico or Texas. *N. albigula warreni* and the northern populations of *N. micropus canescens* are probably most like the common ancestral stock from which these two species diverged. *N. micropus* and *N. albigula* probably constituted formerly a single rassenkreis that became divided somewhere near the center of the chain into two species. Later the separated subspecies of the chain, *N. m. canescens* and *N. a. warreni,* came into contact again before they had diverged sufficiently to prevent fertile crossing.

N. floridana is not known to occupy the same terrain in Colorado as any other wood rat. However, there is a possibility of contact with *N. micropus* or *albigula* in the Arkansas Valley. Although *floridana* has never been taken south of the Arkansas River and neither of the other species has been taken north of the river in Colorado, I have examined a specimen of *N. micropus canescens* from north of the river just over the line in Kansas (KU 3484 from seven miles northeast of Coolidge, taken by J. M. Linsdale). Because of the similarities of ecological requirements of these three species it is likely that some competition for shelter would take place if *floridana* were to meet either of the other species.

There is a greater possibility of competition for dens between *floridana* and *mexicana.* The western limit of *floridana* seems to coincide with the eastern limit of *mexicana* between Colorado Springs and the Arkansas River, where the High Plains meet the foothills of the Rockies. Although the absence of suitable rock shelter may prevent *mexicana* from spreading out on the plains, there is no evident reason why *floridana* should not spread into the foothills, unless it be the competition of *mexicana* for rock shelters. The western limit of tree cactus and other suitable shrubs at the edge of the High Plains would make conditions for the building of houses by *floridana* less favorable in the foothills than on the plains.

Although the foregoing discussion speaks of competition between different wood rats for den sites, this competition may not take the form of physical conflict between individual rats, in which one ousts the other from its den. Some fighting undoubtedly takes place, but even in the absence of direct conflict one species may be expected to replace the other if the utilization of the same kind of den by both species results in differential death rates and differential reproduction, from whatever cause. The value of a den is determined by the quality of shelter it provides, either against enemies or against adverse weather conditions. Probably only occasionally is adverse weather a factor favoring the survival of one species over another in a given type of den. However, predation is operative almost continually and its relative effectiveness is closely dependent upon the behavioral response of each prey species in relation to the kind of den shelter. There is little direct evidence bearing on the mechanism of competition between wood rats, but what indirect evidence there is points to predation as the dominant selective factor controlling competition and ecologic divergence.

PHYSICAL AND BIOTIC FACTORS CONTROLLING DISTRIBUTION

The six species of wood rats the ranges of which extend into Colorado have widely differing patterns of distribution. No species occurs throughout the state, but one or another can be found in nearly every part of it. Only in the northern part of the Colorado Piedmont and in the San Luis Valley do wood rats seem to be absent.

The southern limit of *N. cinerea rupicola* in northeastern Colorado corresponds with the physiographic break between the rough, broken rim of the High Plains with its outlying buttes, and the wide, nearly flat valley of the South Platte River. The absence of large rock exposures with deep crevices prevents *rupicola* from spreading out on the valley.

The eastern limit of *N. c. orolestes* on the eastern flanks of the Rocky Mountains is probably also primarily determined by topography, although competition with *N. mexicana* may be a factor. These two overlap, between the Wyoming border and Pikes Peak, in a narrow zone on the steep lower mountain slopes between approximately 6500 and 7500 feet, but *orolestes* is ordinarily absent from the foothills were *N. m. fallax* is abundant. High cliffs and vertical crevices preferred by *orolestes* are abundant in the high mountains but less common in the foothills. The abundant ledges, boulders and smaller vertical crevices of the foothills provide ample shelter for *fallax* and might be adequate for a sparse population of *orolestes* if *fallax* were not present. Probably the zone of overlap is one of fluctuating populations of both species, the limits of which at any time depend on varying climatic and other conditions, and competition for den sites.

South of Pikes Peak the line depicting the eastern limit of *orolestes* on the map (Fig. 2) is much less accurate than the line from

Pikes Peak to the Wyoming line. The canyon of the upper Arkansas River from Salida to Canon City may be occupied by *orolestes* as well as *mexicana.* Certainly the high canyon walls are ideal for shelter, but the elevation (7000 to 5300 feet) is a little low for *orolestes.* Perhaps the higher temperatures there give *mexicana* some advantage. Whether or not *cinerea* and *N. mexicana scopulorum* actually overlap or compete along the eastern base of the Sangre de Cristo Range is not known, for both have not actually been taken at the same locality south of the Arkansas River.

N. cinerea has no geographic limit in western Colorado, but there is a line of intergrading contact between *orolestes* and *arizonae* that falls roughly near the 7000 foot contour. *N. c. arizonae* at lower elevations endures higher summer temperatures than *orolestes* and occupies many smaller rock shelters. There are probably physiological, as well as morphological differences between these subspecies permitting *arizonae* to thrive in a hotter drier climate.

The western limit of *N. mexicana fallax* and *N. m. scopulorum* on the flanks of the Rocky Mountains is also the upper elevational limit of the species in Colorado. In Boulder County the highest record is 7500 feet, whereas farther south they occur higher. In southern Colorado Mexican wood rats have been taken at approximately 8000 feet, on Fisher Peak and in the San Luis Hills west of San Acacio. In New Mexico the upper limit is still higher. Bailey (1931: 183-184) reports specimens of *N. mexicana* from 7400 to 8500 feet along the headwaters of the Pecos River at the southern end of the Sangre de Cristo Mountains, from 6700 to 9200 feet in the Magdelena Mountains, and from 7800 to 9000 feet in the San Mateo Mountains. Both of the latter ranges are in central New Mexico west of the Rio Grande. In all these areas the zonal range is the same: Transition and lower edge of the Canadian lifezones. These records strongly suggest that the upper limit of *mexicana* is determined by temperature. Competition with *N. cinerea* for den sites possibly is a limiting factor, but since at higher elevations *cinerea* does not usually occupy the smaller spaces under boulders and low horizontal ledges, which are most suitable for *mexicana,* it seems unlikely that there is any shortage at higher elevations of unoccupied den sites that are adequate for *mexicana.* On the other hand, competition with *cinerea,* where present, could prevent *mexicana* from occupying the high cliffs with deep vertical fissures and caves.

The eastern (lower) limit of *N. mexicana* in Colorado is almost certainly set by topographic conditions. North of the Arkansas River suitable rock shelter for dens is almost non-existent east of the edge of the foothills. Along some of the draws out on the plains, scattered outcrops would be adequate for *mexicana,* but the inability of this species to build adequate houses away from rocks would prevent it from crossing long expanses of plains between suitable rock exposures. An additional difficulty might be competition with *N. floridana,* which already occupies many rock outcrops on the plains.

South of the Arkansas River many small tributary canyons cutting across the plains have provided favorable habitat enabling *N. m. scopulorum* to thrive there. The eastern limit of *scopulorum* is not precisely known but probably follows the limits of fairly continuous canyons and outcrops of the Dakota sandstone. Attempts by Cockrum to obtain *mexicana* in the isolated Dakota outcrops of southwestern Kansas convinced him that this species was not present there. He obtained only *N. micropus* in such situations.

Although the lower Arkansas River is indicated on Figure 3 as the northern limit of *scopulorum,* I am not certain that suitable rocky habitat actually extends to the flood bottom of the river. Scarcity of rock outcrops on the north side of the river and presence there of *floridana* may prevent *mexicana* from becoming established there if it should get across the river. The upper Arkansas River in Chaffee County is certainly not an effective barrier to wood rats, probably because they can cross in the winter on ice.

The Colorado and Gunnison rivers in western Colorado seem to be an effective barrier to the northward and eastward spread of *N. m. inopinata.* (For discussion of specimens from Grand Junction collected by E. R. Warren see page 287.) The Colorado River is also a barrier to the species in Utah (Kelson, 1951: 96) and in Arizona (Goldman, 1937: 434). The sinuous line (Fig. 3) indicating the limit of *inopinata* on the western and southern flanks of the San Juan Mountains lies generally near the 7500 foot level, which is the highest elevation at which a specimen has been taken (locality *20* of Fig. 3). But in the Uncompahgre Valley *inopinata* has not been found higher than 6000 feet (locality *10* of Fig. 3). The records do not indicate any difference in temperature tolerance between *N. m. fallax* and *N. m. inopinata.* The upper limit of *inopinata,* as well as of *fallax,* is probably controlled by temperature. There is no scarcity of suitable rock shelters or of palatable food plants at higher elevations. Competition with *N. cinerea* is even less likely to limit the range of *inopinata* than *fallax,* because *N. c. arizonae* occupies almost the same area in southwestern Colorado as does *N. m. inopinata.* There is habitat separation between *arizonae* and *inopinata* at some localities but not at others. The slight differences in shelter preference between these seem to permit them to occupy the same area.

The distribution of the white-throated wood rat in western Colorado is similar in pattern to that of the Mexican wood rat but more restricted in area. The upper limit of *N. albigula* is close to 7000 feet elevation at the highest, but in some areas lower. Since the divide between the Dolores and San Juan drainages is barely higher than 7000 feet, contact between populations of *N. albigula* in the two drainage systems seems to be intermittent. (See p. 296.) The range of *N. a. brevicauda* in the Dolores River drainage is not fully known, but the limits of *N. a. laplataensis* in the San Juan drainage have been rather closely established. The divide between the Dolores and the San Juan systems probably has partially isolated the population on the Dolores side, thus permitting its differentiation as a separate subspecies.

Cactus and Utah juniper are most abundant below 7000 feet in the same areas of southwestern Colorado in which *N. Albigula* occurs. These plants are the most important food resources for this wood rat, but are probably not indispensible. Since cactus and juniper in moderate abundance occur usually several hundred feet higher than *N. albigula,* the absence of these plants could not be the primary factor affecting the upper limit of *albigula.* Neither could absence of suitable den sites; for horizontal ledge outcrops and fallen blocks are abundant above the limit of *albigula.* The occurrence of *albigula* and *mexicana* in the same habitats at several localities shows that these species are ecologically sufficiently divergent to exclude competition as a factor limiting the range of either. *N. albigula* is even more divergent from *N. cinerea.* Low temperature, or a combination of weather elements in winter, probably accounts for the distributional limits of *albigula* in western Colorado.

The western (upper) limit of *N. a. warreni* in southeastern Colorado is not so well defined as the upper limit of *laplataensis* but seems to follow roughly the eastern base of the Sangre de Cristo Mountains, which is also approximately the western limit of the tree cactus. The highest known occurrence of *warreni* is 6600 feet (locality *17,* Fig. 4). Tree cactus is one of the most used plants both for food and shelter, but *warreni* lives at some places where this cactus is absent. The next most used plant, the one-seed juniper, probably occurs at higher elevations than *warreni*. Shelter, both under rocks and in junipers, seems to be abundant in the foothills. The available information suggests that winter temperatures prevent *warreni* from spreading higher than about 6800 feet.

N. a. warreni is not known to occur north of the Arkansas River, which probably is an effective barrier to this species. Cactus and yucca clumps suitable for houses of *albigula* grow on the south side of the river up to the edge of the valley bottom. Any wood rats living on the bottom might be able to cross to the north side at times of shifting river channels or when nearly all the water is diverted for irrigation. The bottom, however, covered with flood deposits and stands of cottonwoods, is not a favorable habitat for *N. albigula*. The eastern limit of *warreni* on the High Plains is not accurately known but probably does not extend into Kansas. Suitable habitats (tree cactus, clumps of prickly pear, clumps of yucca, or rock outcrops) become smaller and farther apart as one proceeds eastward across Prowers County or Baca County into Kansas. Perhaps *albigula* is unable to cross some of the stretches of inhospitable open terrain frequently enough to maintain colonies in isolated pockets of favorable habitat. Competition with *micropus*, which occurs in the same area and farther east in Kansas, may also be a limiting factor. (The relations of these two species are discussed more fully in the preceding section.)

The Arkansas River is shown on the map (Fig. 5) as the northern limit of the gray wood rat in Colorado, but a single specimen is known from north of the river in Kansas (see above, p. 537). Although the river and its flood bottom are not a complete barrier to the gray wood rat, the individuals that get across may be unable to compete favorably there with *floridana*.

The western limit of *micropus* is probably farther west than shown on Figure 5 and can be established only by additional collecting. Since *micropus* is a species widely distributed in desert and tropical climates, one might suppose low temperatures would prevent the species from living at higher elevations on the western edge of the High Plains. But climate could hardly impose a limit in Otero and eastern Las Animas counties. The chinook winds on the eastern slope of the mountains and the down-valley winds in winter emerging from the upper Arkansas Valley and the Royal Gorge give the foothills and upper edge of the plains a milder climate than that at lower elevations on the eastern border of the state. This chinook effect is shown by the positions of the isotherms for 32° and 34° on the map of average, January temperature (U. S. Dept. Agric., 1941: 804). Perhaps it is significant that the area enclosed by the isotherm for 32° is similar to the range of the tree cactus in Colorado as shown on Cary's map (1911: 241). I know of no reason why *micropus* could not live throughout the plains area south of the Arkansas River.

N. floridana has not been found south of the Arkansas River, but houses probably of this species were reported in the Arkansas River bottom near Holly (locality *20*, Fig. 5). The rats probably are able to cross the river at times of low water, when nearly all of it is diverted for irrigation, or at times of high water if groves of cottonwoods are transferred from one side to the other by shifting stream channels. Any Florida wood rats that overcome the partial barrier of the Arkansas River may be at a competitive disadvantage with the gray wood rat and the Mexican wood rat.

The western limit of *floridana* between Fountain and the Arkansas River seems to coincide with the western edge of the plains and the eastern limit of *N. mexicana.* Perhaps *floridana* occurs farther up the Arkansas Valley in tree-cactus houses or thickets of skunkbush. The climate in the foothills is less extreme than that endured by *floridana* on the High Plains and would not prevent its spread in the foothills. In rocky habitats, however, *mexicana* is probably the better adapted and dominant species. If *floridana* and *mexicana* actually meet, I would expect them to compete for the shelter of rock outcrops and boulders, with the result that *floridana* would not spread outside of the area in which tree cactus is available.

The distribution of *floridana* on the plains is spotty and irregular, generally following creeks and gullys along which occur scattered cottonwoods, clumps of brush, or rock outcrops. Most of the creeks drain southward to the Arkansas River or eastward into Kansas. The wood rats seem unable to cross the nearly flat, featureless interfluve between the Arkansas and South Platte drainages, over which there is almost no cover except grass. The only likely wood rat habitat I saw between the South Platte River and Wray was a line of rock piles and north-facing rimrock called Fremont Buttes, five miles northwest of Akron, Washington County. The numerous rock shelters and dense thickets of chokeberry and golden currant there seemed to provide amply for the needs of either *N. floridana, mexicana* or *cinerea.* Thorough searching, however, revealed no sign that any wood rat had ever occupied the crevices. The outcrop seemed to be too isolated by bare open plains.

The distribution of *N. lepida* in Colorado includes only fingerlike extensions up river valleys at the far northeast margin of the range of the species. Since most of the range of the species covers hotter drier regions at lower elevation, it is reasonable to suppose that the range of *lepida* in the valleys of the Colorado and White rivers may be limited by winter temperature. The highest record of *lepida* in Colorado (6200 feet at locality 2, Fig. 5) suggests that the species should be able to range farther up the White River and Colorado valleys, possibly as far as Meeker and Rifle. There is no deficiency of preferred plants or rock shelter suitable for *lepida* in either valley as far up as Meeker and Rifle. The Colorado River seems to be a barrier to *lepida,* as well as to *mexicana* on the opposite side. But the absence of records of *lepida* from the north side of the White River is probably only due to insufficient collecting. *N. lepida* may be expected to occur also in the region of Yampa Canyon in the dinosaur National Monument.

SUMMARY

Almost every part of Colorado is inhabited by one or more species of wood rat. At some localities in southwestern and southeastern Colorado as many as three species occur in the same or adjacent habitats at low elevations. The bushy-tailed wood rat (*N. cinerea*) is the only species that ranges throughout the high mountains above an elevation of 7500 to 8000 feet.

TAXONOMY AND DISTRIBUTION.—Six species of wood rats (genus *Neotoma*) occur in Colorado—a number larger than occurs in any other state. Each of three species (*N. cinerea, N. mexicana,* and *N. albigula*) is represented by three subspecies; each of the other three species (*N. micropus, N. floridana,* and *N. lepida*) has a single subspecies in the state.

The known range of *N. albigula brevicauda,* previously reported only from the type locality in Utah, has been extended into Colorado up the Dolores and San Miguel rivers to the divide between the Dolores and San Juan drainages, where intermittent contact with *N. a. laplataensis* probably occurs.

Three subspecies of *N. cinerea* are recognized in Colorado: *orolestes, arizonae,* and *rupicola. N. c. cinnamomea* is synonymized with *N. c. arizonae.* Color differences formerly attributed to *cinnamomea* from northwestern Colorado and southwestern Wyoming are based on individuals in the subadult (second) pelage, which is not distinguishable from the same pelage of *arizonae.*

PELAGE AND MOLTS.—Color in wood rats is highly variable with age, season, locality, and species. The taxonomic usefulness of color depends on recognition of the successive pelages of young rats and of the various kinds of variation in pelage coloration.

Young wood rats of most species undergo three molts in their first year. The second and third molts begin usually before completion of the preceding molts. There is only one annual molt in each succeeding year. The pattern of the postjuvenal molt is most regular, the annual molt most irregular. There are minor differences in molt pattern between the species.

COMPARISON OF DENS.—Differences between dens of some sympatric species of wood rats are great enough to permit identification of the dens with almost positive certainty. The dens of other sympatric species can almost never be identified without capture of the occupants. Dens of *N. cinerea* are usually in high vertical crevices in cliffs or caves, whereas those of *N. mexicana* and *lepida* are usually in low horizontal crevices or under boulders or large fallen blocks. Dens of *cinerea* usually contain larger accumulations of sticks and bones.

Dens of *N. albigula* in rock shelter are nearly always in low situations like those used by *mexicana* but differ from dens of both *cinerea* and *mexicana* in having a much greater amount of cactus spines in the midden. Where cactus is scarce on the eastern edge of the range of *N. a. warreni,* dens of *albigula* can be distinguished from those of *mexicana* by the greater amount of juniper needles and/or yucca blades contained, whereas dens of *mexicana* have usually more cuttings of skunkbush and other soft-leaved shrubs.

Houses of *N. albigula* and *N. micropus* in cactus or yucca are indistinguishable, as are dens of the same two species under rock outcrops or fallen blocks. *N. albigula,* but not *micropus,* also frequently builds houses in junipers.

If rock dens of *N. floridana* and *mexicana* occur together south of Colorado Springs, they are difficult to tell apart. Those of *floridana* usually contain more dry stalks, cow dung, cactus joints and spines. Houses of *floridana* resemble those of *micropus* and *albigula* but contain more dry stalks or sticks and less cactus debris.

Two sympatric species of wood rats sometimes occupy the same rock den, probably in succession rather than simultaneously. Such dual use of the same shelter by *mexicana* and *albigula* can be recognized by the distinctive middens left by each species.

Competition.—At many localities a large proportion of suitable shelters are actually used for dens when the population of wood rats is high. If the species is dependent on rocks for shelter, the local distribution of dens is usually in a linear pattern, conforming to suitable rock exposures. Competition between wood rats for den shelter, probably under the pressure of predation, is an important factor limiting populations of wood rats.

Since there is nearly always a greater supply of food available than can be eaten by the largest population capable of finding adequate shelter in the area, there is probably little competition for food.

Ecological Divergence.—Divergent adaptation to different kinds of shelter brought about by competition has been important in the evolution of species of wood rats. *N. mexicana* has the most generalized den requirements and the weakest collecting instinct; consequently it does not build houses and rarely lives away from rock shelter of some kind. *N. cinerea,* particularly *N. c. orolestes,* is the best rock climber and prefers living in the vertical clefts in high cliffs. *N. albigula,* in contrast, prefers to live close to the ground level where it uses for dens the horizontal crevices under low, ledge outcrops and the spaces beneath large fallen blocks and boulders. *N. albigula,* as well as *micropus* and *floridana,* has a strong collecting instinct and often builds massive houses of sticks, cactus joints, and livestock dung. The ability to build houses away from rocks is a specialized trait which liberates the species from dependence on ready-made shelter, usually provided by rocks.

Ecological divergence in food habits has also occurred in the evolution of wood rats. All wood rats in Colorado subsist mostly on relatively coarse, leafy vegetation and cactus pulp, supplemented by seeds, fruits, and other parts of plants. *N. cinerea* and *mexicana* prefer the foliage of soft-leaved shrubs, forbs, and montane conifers, whereas *albigula* and *micropus* prefer the succulent pulp of cactus and the foliage of junipers and xerophytic shrubs and forbs.

Hybridization and Ecological Relationship.—In Colorado the morphological differences between *N. albigula warreni* and *N. micropus canescens* are slight, and occasional hybridization seems to occur between these species in northern Baca County. In New Mexico, *N. a. albigula* and *N. m. canescens* are easily distinguished and probably do not hybridize.

The most reliable characters by which *N. a. warreni* may be distinguished from *N. m. canescens* are: (1) maxillovomerine notch small, (2) temporal ridges bending sharply inward at posterior edge of parietals, and (3) frontal region less arched than braincase and base of rostrum. The most reliable contrasting characters of *canescens* are: (1) maxillovomerine notch absent, (2) temporal ridges smoothly flaring and converging on parietals, and (3) frontal region strongly arched and channeled.

In Colorado *N. albigula* and *N. micropus* occupy the same kinds of houses and rock dens, but only occasionally at the same locality. Farther south these species are ecologically more divergent, *albigula* nesting almost entirely among rocks, and *micropus* almost entirely away from rocks in houses made of sticks, dung, and cactus debris. The ecologic relationship between these species in Colorado, New Mexico, and Texas supports the morphological evidence that populations of *N. a. warreni* and *N. m. canescens* in Colorado are the most closely related populations of these two species, in comparison with other more dissimilar populations farther south. The two species probably belonged formerly to a single rassenkreis that became broken near the center and the broken ends of which later came into contact.

FACTORS LIMITING DISTRIBUTION.—The environmental factors that seem most important in limiting the distribution of one or more species of wood rat in Colorado include the following: (1) low temperatures, (2) river barriers, (3) absence of suitable rock outcrops, (4) absence of suitable cactus or shrubs for house support, and (5) competition with another species of wood rat, primarily for limited den shelter.

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Transmitted April 12, 1957.

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Vol. 10, No. 7, pp. 553-572, 4 pls., 3 figs.
May 4, 1959

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UNIVERSITY OF KANSAS
LAWRENCE
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UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

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Published May 4, 1959

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
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27-7605

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INTRODUCTION

A knowledge of the home range and movements of the cottontail *(Sylvilagus floridanus)* is one of the most important prerequisites for estimating effectively its numbers and managing its populations. By comparing results obtained from different methods, previously used, for determining the size of the home range I have attempted to develop a more valid procedure.

The study here reported upon was made on the University of Kansas Natural History Reservation (Sec. 4, T. 12S, R. 20E), the northeasternmost section of Douglas County, Kansas, approximately 6½ miles north-northeast of the University campus at Lawrence. The 590-acre reservation, situated in the ecotone between the eastern deciduous forests and the prairie of the Great Plains near the north edge of the Kansas River Valley, has been protected as a "natural area" since 1948 (Fitch, 1952). It consists of tree-covered slopes, and flat grass-covered hilltops and valleys. Two limestone outcrops follow the contours about five and 20 feet below the tops of the hills.

The 90-acre study area consists of a valley bordered on the north by a wooded slope and on the southeast by another wooded slope adjacent to a narrow hilltop, east of which is another wooded slope. The area is thus an alternating series of three wooded slopes and two grass-covered, relatively level areas.

The wooded slopes rise from the valley for about 125 feet at a grade of approximately 16 per cent. There is a sharp increase in grade to 36 per cent 100 feet below the top of the hills. A natural terrace 50 feet to 100 feet wide parallels the hilltop at the base of the 36 per cent incline.

The vegetation of the northwest-facing wooded slopes has been described by Packard (1956). It consists of American elm (*Ulmus americana*), shagbark hickory (*Carya ovata*), chestnut oak (*Quercus muehlenbergii*), black oak (*Quercus velutina*), and black walnut (*Juglans nigra*), in that order of dominance. Honey locust (*Gleditsia triacanthos*) and hackberry (*Celtis occidentalis*) are also present. Shrubs and herbs of the lower story include greenbriar (*Smilax hispida*), wild grape (*Vitis vulpina*), Virginia creeper (*Parthenocissus quinquefolia*), coralberry (*Symphoricarpos orbiculatus*), gooseberry (*Ribes missouriense*), bluegrass (*Poa pratensis*), sedges (*Carex* sp.), poison ivy (*Rhus radicans*), and white snakeroot (*Eupatorium rugosum*).

The flat hilltops are covered by a mixture of grasses and forbs but are dominated by awnless brome (*Bromus inermis*). Foxtail (*Setaria glauca*), false redtop (*Triodia flava*), and panic grass (*Panicum clandestinum*) also occur commonly. Awnless brome is dominant in the valley (Pl. 46, fig. 1; Pl. 47, fig. 2) except in the eastern end where bluegrass is dominant (Pl. 45).

Near the tops and bottoms of the slopes barbed wire fences separate the woodlands from the grasslands, which were grazed until 1948. The borderline between woods and grasslands is well defined but woody plants are rapidly encroaching into the grasslands. Young Osage orange (*Maclura pomifera*), American elm, and hackberry are common trees encroaching on the grasslands. The edge vegetation between woods and fields (Pls. 45 and 47) includes smooth sumac (*Rhus glabra*), coralberry and wild plum (*Prunus americana*). The lowland edges are characterized by blackberry (*Rubus argutus*), greenbriar and elderberry (*Sambucus canadensis*). Plates 45, 46 and 47 all show local habitat in situations where traps were actually operated. Fitch (1952: 8-22), Leonard and Goble (1952:1015-1026) and Martin (1956:366-372) have described parts of the Reservation that include the study area.

I am grateful to Professor Henry S. Fitch for guiding my work, to Professor Rollin H. Baker for suggestions and encouragement in the early part of the study, to Mr. Robert L. Packard for certain trapping records that supplemented my own, and to Professor E. Raymond Hall for valuable suggestions. Norma L. Janes, my wife, typed the manuscript. Photographs were taken by me. The State Biological Survey of Kansas provided funds, equipment, and transportation.

METHODS AND TECHNIQUES

Schwartz (1941), Dalke and Sime (1938), Dalke (1937 and 1942), Hendrickson (1936), and Allen (1939) estimated the home range of the cottontail by drawing, on a map, straight lines that connected all marginal points of capture in live-traps. The resulting home ranges were polygonal figures. Haugen (1942) altered this method by drawing lines that connected points midway between the actual points of capture and the next outermost traps in the grid. Fitch (1947) used a method for enclosing all points of capture in a circle or ellipse that represented the home range boundaries and expressed home range as the diameter of these figures. Another method, which has been used to determine the home range of birds, is to map the movements of an individual as it is observed. Stebler (1939) suggested the use of tracking records to determine home range. Connell (1954) expressed home range of cottontails as the average distance traveled from a computed center of activity. The method was originally proposed by Hayne (1949).

The methods used by other investigators to calculate the home range of the cottontail have yielded estimates varying from 0.1 acre to 100 acres. Such wide variations in the estimated size of home range may result from the use of different methods and from insufficient data. The data obtained from live-trapping are not fully adequate because traps cannot sample, in time and space, the entire home range of an individual. Also, "trap habit" or "trap shyness" may distort the apparent shape of the home range. In order to compare these methods I have calculated home range from my data by each of five different methods. The results are shown in Table 1.

No two methods yielded exactly the same results. To utilize all available data for each individual, I recorded on a map the locations of capture in live-traps, nests and forms, locations where the animal was observed in the field and the routes that it took between them. At the end of the study a line was drawn on the map to enclose the areas where the cottontail was known to have been.

Live-traps were operated intermittently at 130 stations between December 8, 1954, and February 10, 1956. Sixteen cottontails were marked in the same area by Robert L. Packard in 1954. Data from 7850 trap nights were used in this study. The traps were set at fifty-foot intervals and the pattern approximated that of a grid in habitat favorable for cottontails such as at edges of woodland. In wooded areas traps were placed at fifty-foot intervals parallel to the edges. Traps were not set on areas of poor habitat where neither cottontails nor their sign were observed.

The traps were operated eight to twelve days and closed for two to five days intermittently throughout the trapping period except in the months of April to August, 1955, when trapping was unsuccessful because the cottontails then were not attracted by bait.

Two kinds of traps were used in my study: those made by the National Live Trap Company and those described by Fitch (1950). Both types performed well and were serviceable under ordinary field conditions. Experiments were made periodically throughout the trapping period to determine which bait was most attractive to cottontails and least attractive to birds, rodents, skunks, raccoons, and opossums. All of these animals hindered operations by stealing bait and springing traps. Corn, scratch-feed, carrots, parsnips, tomatoes, lettuce, apple, cabbage, raisins, sorghum, sugar candy, and onions were used as bait. Corn and scratch-feed attracted cottontails best in all seasons. Corn was superior to scratch-feed, which was quickly stolen by small birds and rodents. Eighty-nine cottontails (40 females, 49 males) were captured in the course of the study.

Cottontails were marked individually at the time of first capture. When necessary, the markings were renewed at later captures; in all such instances the same color codes and numbers were retained for each. Markings were of four types: numbered ear tags, colored ear ribbons, colored tail fur, and colored feet. It was intended to make each individual cottontail recognizable in a trap or in the field. Occasionally when a predator had killed and eaten a cottontail the tail and feet remained and, when dyed, they provided important clues to the identity of the individual. However, the color of the feet is not ordinarily discernible in the field while the rabbit is alive.

Monel metal ear tags (size No. 4, National Band and Tag Co.) were punched through the lateral or posterior fold of the ear close to its base (Pl. 48), one in each ear as insurance against possible losses. However, only three tags were pulled out of the ears and lost in the course of this study. In no instance was identity of an individual cottontail lost. The tags caused no damage to the ears over a period of 21 months.

Trailing in snow is an effective method of studying the daily activities. The record preserved by the tracks becomes somewhat confused after the snow has lain on the ground for more than one night, and after the third night it is impossible to read the surface of the snow. The first day of thaw usually ends tracking because the investigator loses the trail when it crosses a patch of bare ground. The use of a dye on the feet of the individual to be trailed eliminates much of the difficulty of determining which tracks are to be followed. One or more feet can be dyed when the investigator handles the animal in releasing it from the trap. The trail of dyed footprints is distinguishable from all other rabbit tracks in the area. Even when only patches of snow remain, the animal can be followed by checking the edges of the snow for the emerging footprints of the marked rabbit. The same dye is used to color the tails. The color persists in the footprints for about three hours, over a distance of 600 to 800 yards. The animal leaves only a small spot in each footprint, but when it pauses, the mark is large. Red dye makes the most conspicuous mark in the snow.

Thirty-one rabbits were trailed 68 times with one to six records for different individuals. Almost two-thirds of the trailing records pertain to males, which were caught more easily than females while snow was on the ground.

The trail, for both sexes, in those individuals released and followed immediately was longer than in individuals released and allowed to move away before they were followed. The area ranged over by a trailed individual was not significantly greater in either case. The area ranged over was greater by day than by night. Individuals continued to move while being followed in the day, but stopped to forage and look about at night.

Records were obtained by identifying cottontails that I flushed from forms as I walked through the study area, sometimes using a noise-making device or dragging a rope. Regular search was made along the hilltop rock outcrops, under which hiding cottontails could be identified with the aid of a flashlight. Forms in brush piles, and thickets were visited and the inhabitants identified. Other persons, working on the study area, supplied some of the records of cottontails that were seen alive or found dead. Also through binoculars or a telescope I watched movements of undisturbed individuals. Twenty-three individuals were identified 59 times. Nine females were seen 28 times and 14 males were seen 31 times. Sixty-five other individuals were seen, but could not be identified in the field.

MOTIVATION AND EXTENT OF MOVEMENTS

The home range is an area in which an animal carries on its normal activities of eating, resting, mating, caring for young, and escaping from predators. The cottontail establishes a definite home range and may live its entire life within this area, which permits familiarity with food sources, hiding places, and escape routes.

The cottontail usually establishes its home range in the area where it was born, being semi-gregarious and tolerant of crowding. Eight cottontails that were captured and marked as young remained in the area of original capture after becoming adults. Two of them lived 17 months in the same area, two lived 14 months, two lived 13 months, one lived 12 months and one lived eight months. No young were observed to have moved to another home range after they matured, although some may have moved off the study area and thereby escaped observation.

Young become independent and are seen foraging and moving about by the time they weigh 200 to 300 grams, at an age of four to six weeks. They associate with other young of the same litter and neighboring litters, and frequently frolic together. When two to three months old and weighing 400 to 700 grams they begin to live a more solitary life and usually rest alone in forms. Fourteen young between one and six weeks of age never were recorded to have moved more than 150 feet.

The population reaches its peak in August or September; home ranges varying in size from one-half acre (in young ranging in size from 150 grams to 800 grams) to 12 acres, in adults, are superimposed upon each other. In a woodland area of approximately 21 acres 33 cottontails were living together in September, 1955.

As the growing season ends and winter approaches, the amount of food available to the cottontail decreases and the cover becomes sparser (Pls. 45 and 46); predators, disease, and weather take their toll of the young. The survivors must move farther to find adequate food and cover. The home range of the cottontail in the first winter is overlapped by the home ranges of the other members of the same litter, and members of other litters, as the home range is enlarged to approximately its full size. By April the population reached its annual low point; nine of the original 33 cottontails were known to have survived on the 21-acre area of northwest-facing wooded slope south of the pond.

Foremost among the needs of the cottontail are food and cover. Daily movements motivated by these needs are the most frequent and most extensive that it makes. Movements such as are associated with courting and mating, escaping severe weather, escaping from predators, and caring for young are seasonal or irregular in occurrence.

Because the abundant vegetation of summer provides adequate food and cover, movements made while foraging and seeking concealment are less extensive than those made in winter when leafy vegetation is absent and food is scarce. The average length of trails of foraging cottontails was 175 feet per day in summer (11 individuals observed without disturbance) and 325 feet per day in winter (22 individuals trailed or observed without disturbance).

In the spring and summer cottontails forage mostly near woodland edges for grass and herbs, and usually wander no more than 40 feet into the grasslands from the protection of woodland edges and thickets. In autumn and winter cottontails forage in woods and along woodland edges for bark of trees and shrubs and for fallen fruits of trees. Ninety-two per cent of all fecal pellets found in grassland were within 40 feet of cover suitable for cottontails.

Movements made by the cottontail while foraging appear aimless; typical behavior consists of progression with a hesitant gait of two or three hops, a stop to eat, another series of hops and another stop. Footprints made by this movement are about 12 inches apart. With occasional spurts of hopping the individual moves perhaps ten to twelve feet where it stops and begins to eat again. The area in which the individual forages is usually elongated with its long axis parallel to the edge except in areas of uniform habitat (such as large patches of coralberry) where the area covered tends to be more nearly circular. Cottontails observed foraging were estimated to utilize 10 to 20 per cent of the home range area in one evening. Paths or runways are not ordinarily utilized by foraging cottontails.

In seeking protection from predators or from the weather, cottontails move farther in winter than in summer. The average length of trails of cottontails flushed by me in the study area was 80 feet in summer and 210 feet in winter.

When cottontails were released from live-traps they ran an average of 30 feet before stopping to look about. Cottontails always ran toward the densest cover within 50 feet of the point of release. Ten per cent of the cottontails released from live-traps did not stop running until out of sight (always more than 30 feet).

Movements made by cottontails escaping from predators differ from movements made while foraging. The gait is a full run, often eight to ten feet between footprints in snow; the trail is either straight or slightly zig-zag. If possible, the individual will take refuge in a hiding place such as a rock outcrop, brush pile, or thicket. Eight cottontails emerged from such hiding places an average of 22 minutes after the disturbance ceased.

If unable to find a hiding place a pursued cottontail will run 600 to 1200 feet while circling and returning to the area from which it ran. If not closely pursued, it will usually (in 68 per cent of the instances) not enter hiding places, but continue to run ahead of the pursuer. Of 70 released from live-traps and followed, 23 sought refuge in hiding places. The others ran slowly (4 to 7 feet between footprints in the snow) with frequent pauses to look and listen; they usually succeeded in keeping out of my sight. Twelve times the trails of cottontails followed in this manner passed near a form, or other resting place; always the cottontails had paused at the resting place, and twice the individual went into the resting place and ran out again when I approached. Resulting trails were almost circular, covering most (70-90 per cent) of the home range; sometimes three or four complete circuits were made. The trails made when I pursued cottontails ranged in length from 800 to 3,000 feet. A trail recorded for an individual on one night was almost identical with another trail for the same individual recorded another night. The cottontail is not easily driven out of its home range. Paths or runways are used by cottontails escaping from predators in dense vegetation along fence lines, in thickets, or brush piles, or in snow that is eight or more inches deep.

Most of the year cottontails rest in forms of grass or brush near woodland edges but in extremely cold or hot weather they seek the greater protection of the woods. Movements are limited to the woodlands in severe weather, especially when deep snow makes travel difficult.

Hilltop rock outcrops on the area provide excellent protection for the cottontail especially from low temperatures and freezing rain or blowing snow. Eighty per cent of the cottontails resting under the rock outcrops were found in severe winter weather. Fifteen per cent were found in severe summer weather, and five per cent were found at times when the weather was not severe. Undercut creek banks and exposed tree root-systems in eroded gullies were favorite hiding places. Brush that had accumulated in the ravines and stream beds also was used for cover by the cottontail.

In heavy rain a cottontail may move along, neither hopping nor running, with its body close to the ground, head low, ears laid back. Losing its customary alertness it may pass a person without seeing him. At times, I have been able to approach almost close enough to seize one of the miserable creatures. In deep snow cottontails may progress with long bounds carrying them high enough vertically, to clear the surrounding snow.

Courting activities were seen only in evening. Four male cottontails and three females were observed to move an estimated 1200 feet in an evening (1¼ hours) while chasing each other around in an area of less than an acre. It is presumed that this activity was in addition to normal movements made while foraging.

Seven females known to be pregnant or lactating were not observed to move more than 100 feet away from their centers of activity. Their nests were never found. At the same time the males were moving over much larger areas.

The cottontail is most active in the evening or early morning.

Of those for which time of capture in live-traps was known 70 per cent were captured in the evening between dusk and 11:00 P. M., 10 per cent were captured between 11:00 P. M. and dawn, and 20 per cent were captured after dawn. Nocturnal rodents and carnivores often stole bait in the night; the percentage of capture of cottontails after dawn might have been larger had bait remained in all the traps.

Except for those flushed, cottontails were seldom seen by day. In walks through the study area approximately three times as many cottontails were flushed at night as in the daytime. On cloudy days cottontails were active longer than on bright days. On dark nights more cottontails were captured in live-traps between 11:00 P. M. and dawn than on bright moonlight nights.

Cottontails were more active (as determined by trap success and frequency of observation) at temperatures between 0° F. and 33° F. than at temperatures between 33° F. and 55° F. Activity of the cottontail increased as the temperature of the air decreased. Activity increased in proportion to the percentage of ground covered by snow. Activity of the cottontail decreased as precipitation increased; there was less activity in rain than in snow and less activity in wet snow than in dry snow. Activity did not vary significantly with depth of snow until snow was more than 8 inches deep, when activity decreased abruptly.

The average of the longest distance traveled between captures for cottontails whose entire home ranges were thought to have been sampled was 900 feet for males and 684 feet for females. The average of the maximum distance across the home range for cottontails whose home range had been thoroughly sampled was 1019 feet for males, and 936 feet for females.

The home range is used by the cottontail in different ways, depending on the needs of the individual and the condition of the habitat. In uniform habitat the home range is roughly circular and is used most near its center and least toward its periphery. The entire home range is traversed every four or five days. The center of the home range has been called the "center of activity" (Connell, 1954).

In habitat of alternating woodland and grassland, such as that on the University of Kansas Natural History Reservation, two centers of activity often developed in the home range of a cottontail, at opposite edges of a tract of woodland. The individual concentrated its movements near one center for three to five days then moved to the other center. Pursuit by a predator, random move-

Fig. 1. "House Field" viewed from the northeast corner, looking southwest, March 3, 1956, showing the condition of vegetation in winter. Traps were operated on a 50-foot grid throughout this area.

Fig. 2. Same area as above, on July 10, 1956, showing the condition of vegetation in summer.

FIG. 1. View southeast from the north edge of "Picnic Field" showing condition of the vegetation on December 3, 1954. Trap lines were placed along woodland edge from which this picture was taken, along road where vehicle is parked, along creek beyond road, along edge of field beyond creek, and along edge of woods in background.

FIG. 2. Summer aspect of the vegetation, on July 14, 1955; same view as shown in Fig. 1.

FIG. 1. Condition of vegetation along woodland border northeast of Reservation headquarters on December 3, 1954. Camera was facing southwest. Traps were operated along this edge and in woods to right and in background.

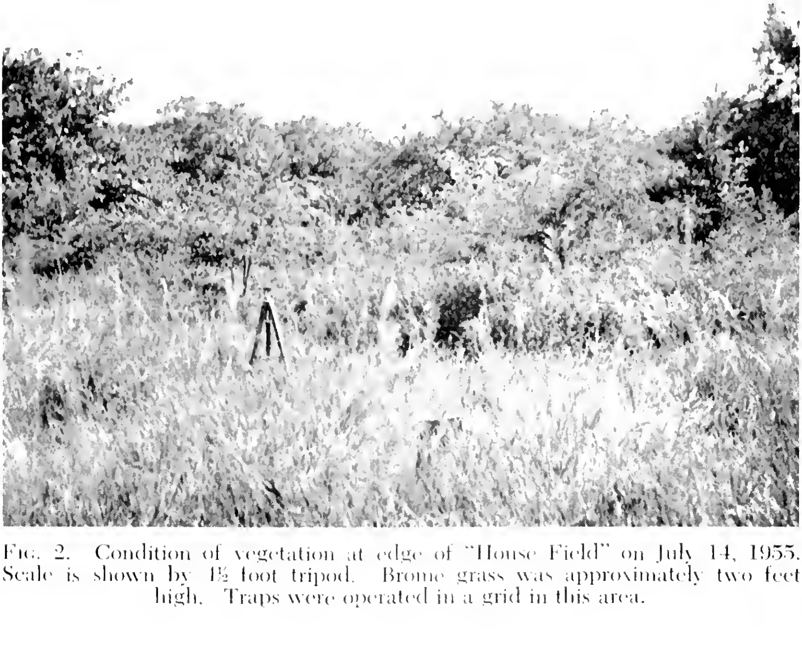

FIG. 2. Condition of vegetation at edge of "House Field" on July 14, 1955. Scale is shown by 1½ foot tripod. Brome grass was approximately two feet high. Traps were operated in a grid in this area.

PLATE 48

FIG. 1. Cottontail in bag with ear protruding, ready for marking with nylon ribbon and metal ear-tag shown in upper right hand corner. × ¼.

FIG. 2. Cottontail bearing ear-tags and ribbon. × ¼.

ment, or other cause may be responsible for shift from one edge to another.

When moving undisturbed through the woods cottontails usually do not pause to forage or associate with other cottontails, but keep to a straight route except in severe weather, when, as noted above, they find resting places in the woods. Ninety-two per cent of the cottontails captured in live-traps were captured within 100 feet of a woodland edge; six per cent were captured in the woods, more than 100 feet from an edge, and two per cent were captured in grassland more than 100 feet from the edge. In winter, when the air temperature was less than 20° F., 22 per cent of the cottontails were captured in the woods more than 100 feet from the edge.

The maximum distance between two centers of activity of an individual was 700 feet, average 550 feet. If two centers of activity were maintained, the cottontail usually traversed the entire home range every seven to 11 days.

In no case was a cottontail known to have lived in two woodland edges which were separated by open grassland. Cottontails usually did not move more than 75 feet from suitable cover. In winter when herbaceous vegetation was dormant cottontails did not cross open fields.

Forms in grass clumps were the usual resting place for cottontails, but others in brush piles, rock outcrops, and tree stumps were also used. On the average a cottontail maintained 3.5 forms. If disturbed repeatedly at a form, a cottontail would permanently desert it. On seven occasions a cottontail used a form that had been used by another within 24 hours. Three cottontails used the same shelter under a rock ledge in five days; one was under the ledge on December 17, 1955, and another was there on December 18. The first was there again on December 20 and a third was there on December 21. The original cottontail had returned by January 2, 1956. There may be 20 to 30 resting places used by cottontails within a single home range area since five to seven cottontails may live there as co-occupants at one time. Two cottontails, both males, lived together in a *Smilax* thicket for three weeks, resting within 15 inches of each other. Occasionally a female was present in the same thicket, and rested about three feet from the males.

A male trapped on land adjoining the Reservation and confined overnight at the Reservation headquarters escaped the next day and was seen 32 days later, 1800 feet from the point of escape, back in the area where it was originally captured.

A female confined for observation, escaped and ran in the direction opposite from her home. Subsequently she was seen on four different occasions, over a period of one month, in her original home range, 1,100 feet from the point where she escaped. Both these animals which made homing movements had been removed in cloth bags from their homes.

Another cottontail removed from its home range and taken to the laboratory building to be marked, escaped and ran to a nearby wooded hillside without pursuit where it could be observed because of snow on the ground and lack of leaves on the trees. The animal ran and hopped about over a one-half acre area. Its movements seemed to be unoriented and it frequently stopped and stood on its hind legs in order to look about. After 10 minutes of this behavior, a red-tailed hawk (*Buteo jamaicensis*) screamed as it flew overhead. The cottontail, stimulated by seeing and/or hearing the hawk, ran faster, moving in circles until it disappeared from view five minutes later. When last observed the cottontail was 1,700 feet from its home range and was headed in the opposite direction. It had passed several potential shelters but had not attempted to use them, presumably because it was not familiar with the area. Although for several months afterward traps were operated in the cottontail's home range area and in the area where it escaped, the animal was never recaptured.

SIZE AND SHAPE OF HOME RANGE

Of the 89 cottontails observed in the study, 35 were captured in live-traps only once and were never seen in the field or trailed. The remaining 54 served for calculation of home range by one or more methods. The minimum, maximum and average home ranges for these 54 individuals were calculated by each of five methods. All individuals for which any area was recorded were included in the average. Incomplete home ranges lower the averages. According to the most reliable method (Composite Method) 30 male cottontails had home ranges of between 0.46 acre and 12.19 acres and 24 female cottontails had home ranges of between 0.46 acre and 12.62 acres. The average for males was 5.05 acres and the average for females was 4.81 acres. The average for all 54 cottontails was 4.86 acres.

Because of irregularities in live-trapping and field observation some cottontails were more intensively studied than were others; one cottontail was followed one time only, while another was trapped 26 times, followed three times, and seen in the field six times. It was necessary to determine which cottontails had been studied sufficiently to determine the approximate extent of their home ranges.

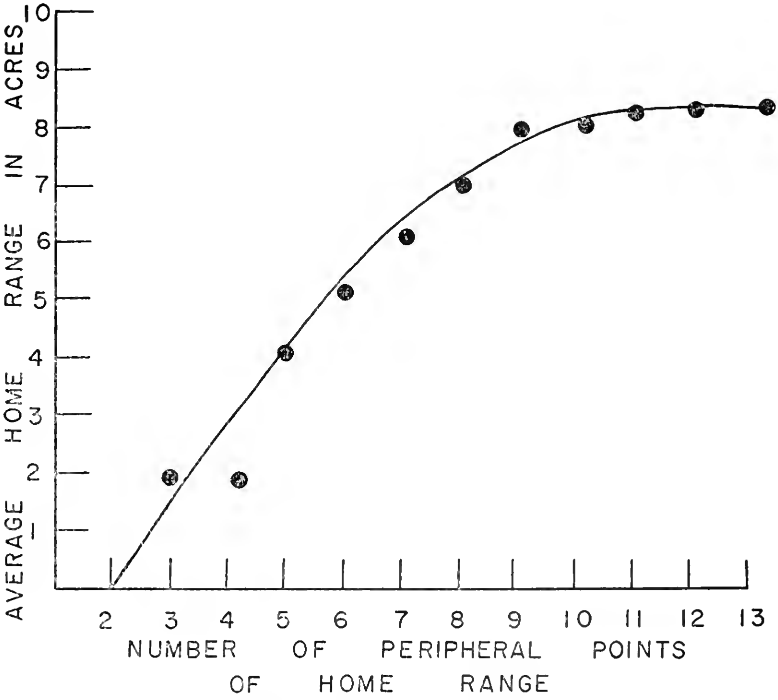

FIG. 1. Correlation between average size of home range and number of "peripheral points" (marginal records, which form angles when the range is outlined). On the average, a sufficient number of records to yield approximately nine peripheral points must be obtained before the full extent of the home range is revealed.

The average area, in acres, of home range was plotted, on a graph, against the number of peripheral points (Figure 1). When a home range had nine or more peripheral points, on an average, the size of home range did not increase significantly with additional captures, observations in the field, or records of trails. Home ranges with less than nine peripheral points were likely to be increased in size with each new observation. A similar situation has been shown by previous authors who have plotted the size of home range against number of captures in live-traps, where only live-trapping was used to gather data. Therefore, in my study, home ranges with nine or more peripheral points were considered to be adequately studied.

Data for eighteen cottontails that had been studied sufficiently to determine the full extent of their home ranges were used to calculate minimum, maximum, and average home range by each of five methods (Table 1). The methods used by Schwartz (1941), Dalke and Sime (1938) and Allen (1939) yielded results which were lower than any others, presumably because only live-trap data were used and because straight lines were used to connect traps in which cottontails were captured. The "composite method" was considered the most reliable because it utilized all data gathered for each individual and because with this method the home range boundaries were drawn to enclose all areas in which the cottontail lived and excluded all areas in which the cottontail was not known to have been. The method used by Fitch (1949) agreed most closely with the "composite method" and suggests to me that the home range of animals can be estimated with reasonable accuracy by this method when field observation or trailing are not feasible. The composite method is superior to others for studying the home range and movements of cottontails.

Of the individuals whose entire home ranges had been thoroughly studied, nine males had home ranges of between 4.72 acres and 12.19 acres with an average of 8.92 acres; nine females had home

TABLE 1.—HOME RANGES, IN ACRES, OF 18 COTTONTAILS ON THE RESERVATION IN 1956, COMPUTED BY FIVE DIFFERENT METHODS.

METHOD	Sex	Number of individuals	Average area	Maximum area	Minimum area
Allen (1939), Dalke and Sime (1938) and Schwartz (1941)	♂	9	2.00	6.78	.30
	♀	9	2.54	7.20	.35
	all	18	2.27	7.20	.30
Fitch (1947)	♂	9	4.01	12.89	1.05
	♀	9	5.68	11.50	1.84
	all	18	4.85	12.89	1.05
Fitch (1949)	♂	9	7.20	....	....
	♀	9	9.00	....	....
	all	18	8.40	....	....
Tracking and field observations	♂	9	8.74	11.15	3.54
	♀	9	8.62	12.18	5.51
	all	18	8.69	12.18	3.54
Tracking and field observations plus live-trapping	♂	9	8.92	12.19	4.72
	♀	9	7.76	12.62	2.42
	all	18	8.34	12.62	2.42

ranges of between 2.42 acres and 12.62 acres with an average of 7.76 acres. The average size of home range for both sexes was 8.34 acres (Table 1).

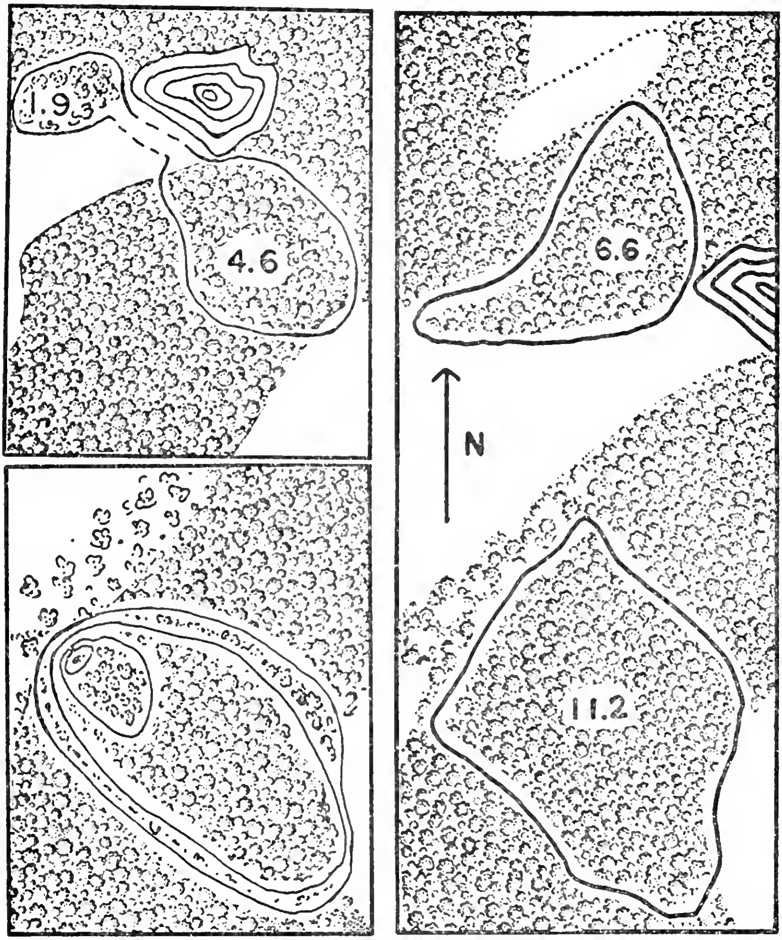

FIG. 2. Maps showing home ranges of cottontails in relation to woodland and open fields on the study area. One inch equals approximately 470 feet. Each home range is shown slightly rounded from the polygonal figures obtained by connecting actual points where the animal was recorded. *Upper Left.* An area of 4.6 acres occupied by a cottontail in winter, increased to 6.5 acres in summer by the animal crossing a narrow grassland strip to another woodland edge. *Lower Left.* Showing increasing size of home range of a female cottontail; in July, 1954 (at age of three weeks), she had a range of .25 acre; September, 1954, 1.5 acres; December, 1954, 8 acres; and December, 1955, 11 acres. *Right Half.* Two home ranges of a cottontail which moved from its original area to occupy a new one 410 feet farther north across a field in September and October, 1955.

Cottontails range over a larger area in summer than they do in winter because suitable cover and food is more abundant in summer. One cottontail (Figure 2, upper left) lived in a woodland home range of 4.6 acres in the winter but increased the range to 6.5 acres in summer by crossing the narrow overgrown end of a field to another woodland area. Another cottontail (Figure 3, top part) lived in a woodland home range of 7.9 acres in winter but in summer increased the home range to 9.5 acres by including also a part of an adjacent field. Other cottontails increased their home ranges in summer by five to 15 per cent.

On the average, male cottontails had a larger (by 13 per cent) home range than females probably because of the increased activity of males in the breeding season and the decreased activity of females when pregnant and caring for young. Nevertheless, some of the largest home ranges measured were those of females.

The size of the home range in immature cottontails varies between 0.1 acre and 4.0 acres, depending on the age and size of the individual. Fourteen young cottontails between three and six weeks of age did not leave areas of approximately one acre in each instance. Nine cottontails between six weeks and 18 weeks of age lived in areas of about two acres. By the time cottontails are four to five

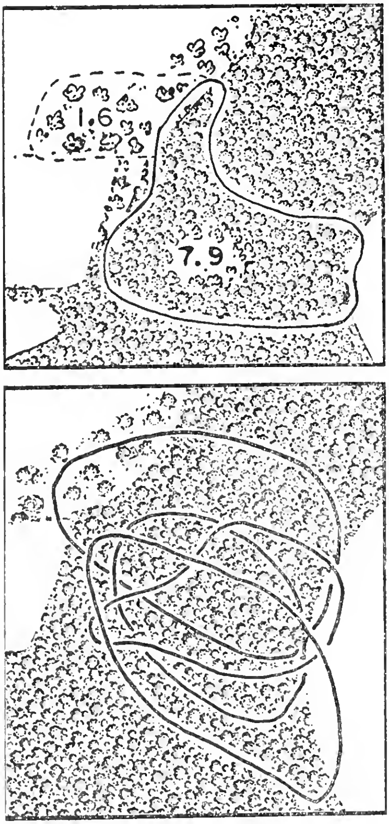

FIG 3. Diagrams showing home ranges of cottontails in relation to woodland and open fields on the study area. One inch equals approximately 545 feet. Each home range is shown slightly rounded from the polygonal figures obtained by connecting actual points where the animal was recorded. *Upper.* Winter range of 7.9 acres (solid line) increased to 9.5 acres in summer by area in dashed line. *Lower.* Overlapping home ranges of four of the many cottontails living on the study area. Each of the four cottontails occupied approximately the same home range throughout the year.

months old they inhabit a home range of four to eight acres.

One cottontail (Figure 2, lower left) born in July, 1954, was estimated to have wandered over approximately 0.25 acre at an age of three weeks. In September this cottontail occupied a home range of one and one-half acres. By December it was five months old and occupied an area of about eight acres. In the next year it enlarged its home range to 11.5 acres.

The cottontail usually settles down in one area and stays there until it dies. Changes from one home range to another are unusual, but minor shifts, in response to changes in vegetation and weather, are common. In one exceptional instance (Figure 2, right) a male cottontail, occupying a home range of 11.2 acres in a woodland, suddenly shifted to a new area that barely overlapped its former home range at one edge. Two months after the change was first noticed the cottontail was living in a new home range of 6.6 acres 300 feet from its original home range. In changing from one home range to the other the cottontail traveled along a dry stream bed and was captured there three times.

Maps of the home ranges of four of those 18 cottontails for which sufficient data were collected to determine the size of home range are shown in the lower part of Figure 3.

SUMMARY AND CONCLUSIONS

The home range and movements of the cottontail were studied on a 90-acre area of the University of Kansas Natural History Reservation from February, 1954, to March, 1956. Eighty-nine cottontails were identified in the field 59 times, trailed 70 times and captured in live-traps 326 times in 7,850 trap nights. Home range of the cottontail was calculated by five methods, using the same set of data, and the results were compared. A composite method was used, which permitted the use of more data than any other one method.

The maintenance of a home range is of survival value to the cottontail. Knowledge of the home range is of value to man when control or propagation of cottontail populations is desired. Cottontails establish a home range where they are born and enlarge it to nearly full size the first winter. Home ranges of cottontails are overlapped by those of others regardless of sex or age. No territory is maintained.

The cottontail makes movements to forage, to seek cover from predators and the weather, to reproduce, build nests, care for young, keep pace with changes in vegetation through the year, and escape unusually severe climatic conditions. Movements may be caused by desire for acquaintance with surroundings and other animals, escape from undesirable surroundings or animals, or merely release of nervous energy.

When foraging, cottontails moved 175 to 325 feet per day, mostly near woodland edges, and used from 10 to 20 per cent of the home range. When escaping from predators cottontails moved 30 to 1200 feet and used 5 to 70 per cent of their home ranges, depending on the type of pursuit. Some cottontails that were followed, ran in almost circular courses for as far as 3000 feet and covered as much as 90 per cent of their home ranges. Paths or runways were not used except in deep snow or very dense vegetation. Movements were limited by deep snow. When temperatures were unfavorably high or low, cottontails sought cover deep in the woods or under rock outcrops, and in dry stream beds. In moderate weather resting places in grass forms, brush piles and thickets were used.

Both males and females moved farther in the breeding season than in the rest of the year, but females that were caring for young in summer and late spring moved shorter distances than they did when not so engaged in autumn and winter.

Cottontails were most active at dawn and especially, dusk, and were more active on dark nights than on moonlight nights. Cottontails were most active when the air temperature was between 0° F. and 33° F. and when rain was not falling. Activity increased as the percentage of ground covered by snow increased and as the abundance of food decreased. Activity did not vary with physiological condition except that as body weight decreased activity increased—probably because of lack of food.

The home range is used most intensively near centers of activity that are near woodland edges or in other areas of good cover. Cottontails often ranged through the woods and along edges but did not cross open areas more than 75 feet wide. Cottontails use their home range most intensively in winter when they are forced to move long distances in poor cover, searching for food. More than one cottontail may use sites of good cover at the same time and two or three used the same resting place at different times.

Two instances of homing were observed; cottontails moved 1,100 and 1,800 feet to return to their home ranges, but one cottontail that escaped 1700 feet from home failed to return.

The average home range of 18 cottontails for whom adequate data were gathered was 8.34 acres. The home ranges of males averaged 1.16 acre larger than those of females. In summer, cottontails increased their home ranges 5 to 15 per cent by taking advantage of cover provided by the more abundant vegetation. Cottontails three weeks to five months of age lived in home ranges of between 0.1 and 4.0 acres and enlarged their home ranges almost to their ultimate full size in the first winter.

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27-7605

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Vol. 10, No. 8, pp. 573-585
October 8, 1959

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UNIVERSITY OF KANSAS
LAWRENCE
1959

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Volume 10, No. 8, pp. 573-585
Published October 8, 1959

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1959

27-9040

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The Sacramento Mountains Salamander, *Aneides hardii* (Taylor), is a plethodontid of relict distribution in the spruce-fir vegetational formation from 8500 to 9600 feet elevation in Otero and Lincoln counties, New Mexico. The salamanders on which most of this report is based were collected three, four, and six miles northeast of Cloudcroft in the Sacramento Mountains. Additional individuals were collected on the eastern slope of Sierra Blanca, 1.5 miles southwest of Monjeau Lookout, at about 9000 feet, Lincoln County, and in the vicinity of Summit Springs and Koprian Springs, 9300 feet, Capitan Mountains, Lincoln County. Certain details concerning the populations in Lincoln County will be reported elsewhere (Schad, Stewart, and Harrington, Canadian Jour. Zool., in press).

We would like to thank Mmes. Donna Schad and Lora Lee Johnston, Messrs. Robert Stewart, Frederick Harrington and Ralph Raitt, and Dr. Robert Selander for assistance in the field, Dr. W. Frank Blair and Dr. Marlowe Anderson for the use of specimens in their care, and Dr. A. Byron Leonard for the identification of the molluscan food items.

In the summer rainy season *A. hardii* lives in and under downed timber and under talus accumulations. Occurrence, however, seems to be partly subterranean and always local; seemingly good habitat frequently appears to lack the animals. Our observations and collections were made in July, August, and September in 1956, 1957, and 1958. Two hundred seventy-seven individuals were taken; these were measured, sexed and examined for breeding status. The food and parasite content of the guts of a few individuals was determined. Thirteen salamanders were kept for varying lengths of time in captivity. The specimens are now stored in collections at New Mexico State University, University of Texas, Museum of Vertebrate Zoology, and the Museum of Natural History, University of Kansas.

The primary study and collecting sites were four and six miles northeast of Cloudcroft, Otero County, at 8600 to 8800 feet in elevation. Vegetation was either almost pure stands of Englemann spruce (*Picea englemanni*) or mixed stands of spruce, Douglas fir (*Pseudotsuga taxifolia*) and white fir (*Abies* sp.). At each locality small oaks (*Quercus*) were present among the dominant conifers. Most of the salamanders found were in downed Douglas fir logs; some were taken from spruce and others from cracks in a variety of deadwood. In the less deteriorated logs the salamanders lived under the loose bark or in small cracks and chambers near the inner bark surface. In large fir logs in advanced stages of decomposition, salamanders could be found to the very centers. This kind of log was apparently highly favorable for salamanders, for it was in such sites that we found notably large numbers of the animals and most of the clutches of eggs that we collected; this kind of log is not frequently found, for its wood is saturated with water and completely punky and nearly ready for final collapse.

In winter, salamanders that spent the summer at the surface presumably move to subterranean cavities, or, at least, to sites away from winter freezing. In December, 1957, and April, 1958, four feet of snow covered our collecting sites, and the downed logs contained ice. A few logs were wet at the surfaces where sunlight hit them, but just under such melt they were icy. On May 3, 1958, snow was in isolated drifts and the centers of the logs were still icy. On May 31, and June 22, 1958, there was no ice anywhere, but no salamanders were evident. Late June is, however, around the earliest time that *A. hardii* emerges (Taylor, 1941).

Food and Foraging Behavior

We identified the contents of stomachs from 16 salamanders collected in 1956 and 1957; the items found in them are listed in Table 1. It is not likely that this list is complete for prey species because *A. hardii* eats a variety of food and probably takes prey almost indiscriminately if it is of appropriate size. The kind of food most frequently eaten was ants; they comprised almost 40 per cent of the total items. Nevertheless, less than half the stomachs contained ants; this may mean that salamanders do not make an effort to take ants over any other prey. Such foraging behavior would result in random capture of ants, and it is noteworthy that the frequency distribution of ants in stomachs suggests a Poisson distribution, a mathematical description of one kind of random distribution.

Adult and larval beetles comprised about 28 per cent of the total items, but were found in only seven of the stomachs. Beetles

TABLE 1.—NUMBERS OF FOOD ITEMS FOUND IN STOMACHS OF 16 SPECIMENS OF ANEIDES HARDII

ITEMS	Individual animals	Percentage of total (154) individuals	Number of stomachs in which found
Mollusca			
Pupilla muscorum *Gastrocapta* sp.	3	1.9%	4
Vallonia pulchella?	4	2.5	
Arthropoda			
Arachnoida			
Arachnida	15	9.7	9
Acarina	13	8.4	3
Insecta			
Orthoptera (*Ceuthophilus*)	2	1.3	2
Hemiptera	1	0.6	1
Coleoptera			
adults (carabids and buprestids)	8	30.9	7
larvae	38		
Hymenoptera			
ants	62	40.2	7
wasps	2	1.3	2
Unidentified	5	3.2	5
Total	154	100.0	

eaten were small representatives of beetle groups likely to occur in or under logs. A relatively large species of spider was found in nine stomachs; it represented only ten per cent of the items taken but was one of the most important foods when mass is considered.

Two adult salamanders not included in Table 1 were found, in the course of examination for parasites, to have empty stomachs. One was a male, and the other was a female taken from a chamber that held an egg cluster. It would not be surprising regularly to find stomachs empty in "incubating" females, but the fact is that the one other such female collected by us had a small amount of food in the gut; probably these individuals take anything that enters the egg chamber, but do not leave for active pursuit of food.

Foraging behavior of captive salamanders was observed by one of us. The salamanders were maintained in a seven-gallon aquarium, the floor of which was covered with soil, mosses, liverworts, certain flowering plants, and pieces of rotten fir log. The salamanders were placed in the terrarium in September, 1956, July, 1957, and October, 1958; one individual lived 13 months, another 14 months.

A variety of natural foods was present in the soil and plant matter placed in the terrarium, and these were presumably eaten as found by the salamanders. However, the great bulk of the food used by the salamanders was introduced for them, in the form of colonies of *Drosophila melanogaster* in half-pint milk bottles. We tried to keep thriving colonies of flies, primarily of the mutant vestigial-winged type, present in the terrarium; in 1957 this was successful to the extent that there appeared to be a surplus of food available at all times. We did not attempt to feed the salamanders any wholly artificial food, such as ground beef.

Initially, the salamanders, although seemingly healthy and well-fed, were not fat. Those that we maintained on a presumably minimal diet remained slender and did not grow in length. Two individuals captured in 1957, however, were maintained on food in excess, and these grew in length and in girth; from an initial size of about 37 mm. snout-vent length (a subadult size) they attained about 45 mm. snout-vent length (an adult size) in a period of five months. The observations on foraging behavior were made primarily on these latter individuals.

The salamanders captured prey by pursuit. A salamander would pursue a fly until it was caught, or until it moved out of the field of action. The salamanders were attracted by movements of flies, and ignored those that were completely quiet; predation was oriented almost wholly on a visual basis. Once they were within 2 to 4 mm. of a fly they would snap out the tongue to secure the fly; they were successful in capturing vestigal-winged flies in about 75 per cent of all tries. The relative success of capture was greater when the animals were fresh from the field and less after they had become fattened. The vigor of their pursuit also decreased noticeably once they became fat. About two days after any new fly colony was placed in the terrarium, a salamander would take up a position just inside the lip of the milk bottle, which was placed on its side. From this vantage point the salamanders took heavy toll of the fly populations, eating both adults and larvae.

Initially the salamanders foraged indiscriminately in daylight or in darkness. Later, as they became fat, they avoided high light intensity and were active only at night or under artificial light of low intensity. The latter pattern of activity is probably typical of the pattern they maintain under natural conditions. Certainly we never saw individuals abroad in daylight at Cloudcroft, yet under favorable environmental conditions they were to be found in sites that required considerable movement over open areas of the ground surface.

For several months two individuals of *Eurycea longicauda* were kept in with *A. hardii.* Foraging of these two plethodontids is nearly identical, but the tongue of an adult *Eurycea* can be extended somewhat more than one-half inch in capturing flies; for *A. hardii* this distance is usually less than one-quarter inch. The relatively short tongue of *A hardii* can be correlated with its life in restricted, subsurface chambers, where prey most frequently is close to salamanders; *E. longicauda* inhabits significantly more open sites.

Parasites

Thirty of the adult *Aneides* collected were examined for parasites; most were parasitized by two species of nematodes, *Oswaldocruzia* sp. and *Thelandros* sp. The former is found in the anterior part of the small intestine and occasionally in the stomach, and the latter occurs in the rectum. There were no gross intestinal pathological changes in the salamanders resulting from parasitism. In fact, no pathological or structural abnormalities were noted in any of the salamanders examined. We believe the two nematodes are well-tolerated by the salamander.

TABLE 2.—OCCURRENCE OF PARASITIC NEMATODES IN ANEIDES HARDII

	Per cent of salamanders infected	Number of nematodes per host		Per cent of nematodes that were immature	
		range	mean	July	Aug.-Sept.
Oswaldocruzia sp....	83	2–15	3.6	100	20
Thelandros sp.......	90	1–17	3.3	64.6	5.7

The numerical and temporal occurrence of the nematodes is summarized in Table 2. It should be noted that of the 17 worms constituting the maximum infection by *Thelandros,* only one was an adult worm; the maximum number of adult *Thelandros* in any one host was five. Similarly, the heaviest *Oswaldocruzia* infection, 15 worms, consisted of immature individuals; the maximum number of adult worms in any one host was ten.

The monthly variation in the relative occurrence of young stages *versus* adult in both nematodes (Table 2) suggests that the parasites are eliminated from hosts sometime in the long period, late September to early June, when *A. hardii* exists subterraneously; the worms thus would be reacquired annually when the salamanders resumed living on the "surface" or near the surface. Table 2 shows that the majority of the worms are immature (100 per cent, in *Oswaldocruzia*) in samples taken in July. Additionally, all but one individual of those constituting the 20 per cent occurring as immature *Oswaldocruzia* in the period August to September were actually collected in early August. These were found in one salamander, and this constituted the heaviest infection for the period; crowding effects may have led to retardation of development of the worms.

If it is true that parasites are reacquired each spring—we assume that no temperature factors or immune reactions are delaying development of the worms, and no unusually long external ovic or free-living phase is a necessary part of their life-history—then the host-parasite data can be used as a basis for hypothesizing about the winter life of the salamander. During "surface" life the incidence of parasitism is high (90 per cent and 83 per cent: see Table 2), indicating that salamanders are readily invaded in times of activity. Salamanders examined in September were all parasitized and probably carried nematodes with them into their winter retreats. This part of their habitat should thus be contaminated with infective stages of both parasites. Yet the salamanders seem to become re-infected when the period of summer activity starts (note the high incidence of immature parasites in salamanders taken in July); therefore, the salamanders lose their worms in winter. This suggests that during their subterranean life salamanders are inactive, and avoid ingestion of infective stages of the parasites. A fairly complete hibernation such as we suppose they undergo has been reported by Szymanski (1914) for *Salamandra* on the basis of kymographic records of movement.

Characteristics of Breeding

Sex-ratio

Tables 3 and 4 show the distribution of sexes for two subsections of our sample. The ratio of males to females in the total sample was nearly 1:1. There were differences in ratios between the three general localities: the two northerly sites had fewer females than males, when compared with the Cloudcroft samples. This is true for the samples of adults, but not for the juveniles, where in each instance the females predominated. We cannot absolutely explain these differences in ratios. Possibly the data on adults reflect different patterns of activity among the sexes so that adult females are simply not present in numbers where we looked for them. They could be located underground, in connection with "incubating" duties; if this is true it would account for the fact that so few egg-clusters have been found in logs.

TABLE 3.—SEX RATIOS IN ANEIDES HARDII, TOTAL SAMPLE

LOCALITY	Number of males	Number of females	Ratio of males to females
Capitan Mountains	35	31	100:87
Sierra Blanca	28	21	100:75
Sacramento, 1958	23	28	100:121
Sacramento, '56-'57	34	43	100:126
All	120	123	1:1

TABLE 4.—SEX RATIOS IN ANEIDES HARDII, ADULTS

LOCALITY	Number of males	Number of females	Ratio of males to females
Capitan Mountains	35	19	100:54
Sierra Blanca	22	7	100:32
Sacramentos, 1958	15	14	100:93
Sacramentos, '56-'57	22	16	100:73

TABLE 5.—AGE RATIOS. ADULTS-JUVENILES

LOCALITY	Number of adults	Number of juveniles	Ratio of adults to juveniles
Capitan Mountains	57	15	100:26
Sierra Blanca	30	22	100:73
Sacramentos, 1958	42	30	100:71
Sacramentos, '56-'57	46	35	100:76
All	175	102	100:58

Age-ratio

The data in Table 5 show adult salamanders to outnumber young at each collecting locality. This is probably not an accurate reflection of actual age composition in this species. Yet, we obtained the same general result in all three years of the study. We assume, therefore, that young were located where we could not catch many of them; probably they were underground. Sites of hatching and of the activities of early life would thus occur where we think the bulk of eggs are laid.

For purposes of this study we had only to age the individuals into adult and subadult classes. The criterion for adult status was breeding capability. A five-millimeter testis was the smallest size found in individuals that probably bred, and all of these were 40 mm. or more in snout-vent length. We arbitrarily considered individuals smaller than 40 mm. to be subadult. This probably does injustice to reality (females were treated the same way), but it should be noted that any error introduced in this way was almost certain to have increased the number of "subadults" in the samples. Thus, the hypothesis above based on age-ratios is not auomatically invalid because of improper aging.

Timing of the breeding season

The time in which egg-clusters are deposited is a good rough index to events in the breeding cycle. We found four egg-clusters, one on July 14, 1957, and three on July 27, 1957; the only other eggs taken to date were found in late August (Lowe, 1950:94). Thus, courtship could occur in June, oviposition in July and August, and hatching from August to September. Actually, it is likely that the season is more restricted in time for any one year. Lowe's find was made in a year in which the summer rains were late, beginning in late July (Stebbins, 1951:137), whereas ours were made in a year having abundant and relatively early rainfall, beginning in late June. Microclimatic humidity is of extreme importance to both the salamanders and their food.

We suppose a great deal of breeding activity takes place underground; the chronology of events in such sites may bear no close relationship to those occurring at the surface, yet it is likely that a close parallel would be found. Breeding activities are ordinarily associated in time with greatest food abundance.

Clutch-size

By clutch-size we refer to the number of eggs in laid clusters. We collected clutches of six, four, four and one; adding one more of three (Lowe, *op. cit.*) gives an average of 3.6 eggs per cluster; the average is 4.2 eggs if our clutch of one is discarded on the grounds it was incomplete.

For comparison we have listed (Table 6) clutch-sizes for some other plethodontids. It should be noted that these numbers refer only to eggs deposited in clusters, and not to large ovarian eggs. Thus, *Aneides hardii* has the lowest range in clutch-size of any North American plethodontid on record. It has been noted in other species that low clutch-size is correlated with low productivity, slow population turnover, and long average life-expectancy (Lack, 1954:103-105; Pitelka and Johnston, MS). If this is the case with this salamander, several other features in its environment and habits would tend to reinforce such population structure: the animals are exceedingly well-concealed (they were first described only 17 years ago [Taylor, 1941]), apparently have few natural enemies (one garter snake [*Thamnophis*] was collected within the habitat of the salamander in three years), apparently have few and benign parasites, and abundant and readily available food.

TABLE 6.—RANGES AND MEAN VALUES OF CLUTCH-SIZES IN SALAMANDERS OF THE NORTH AMERICAN PLETHODONTIDAE [1]

	Range	Mean
Desmognathus spp.[2]	11–40	20
Leurognathus marmorata	28	....
Plethodon cinereus	3–13	9
Plethodon spp.	8–18	13
Ensatina eschscholtzii	12–14	13
Hemidactylium scutatum	30	....
Batrachoseps spp.	7–74	....
Aneides hardii[3]	1–6	3.6
Aneides spp.	7–19	13
Stereochilus marginatus	....	57
Pseudotriton ruber	72	....
Manculus quadridigitatus	3–48	....

1. From Bishop (1947) and Stebbins (1951).
2. Clusters of one and two occasionally found in *D. ochrophaeus*.
3. This study, and from Lowe (1950).

Eggs and "incubation"

Our information concerning eggs essentially duplicates that already reported (see Stebbins, 1951). All egg clusters that we found were in small chambers within decomposing fir logs. In each instance the eggs were suspended from the roofs of the chambers. The clutch of six eggs was a compact mass, and the individual suspensory cables of the eggs were intertwined and fused with one another. The clutches of four eggs, although they too were compact clusters, had each suspensory pedicel distinct from the others. The surface of the eggs was lightly moist, but did not glisten with water, and each egg was completely free of the others. The outer coat of jelly of the fresh eggs measured about 6.4 by 5.7 mm. as they hung suspended; sizes were uniform and no egg was notably smaller or larger than the others.

We attempted to keep eggs artificially, but mold destroyed them after 12 days. We had difficulty keeping them wet without inundating them, for the climate at Las Cruces, New Mexico, where we kept the eggs, is exceedingly dry in summer. Until death, embryos were active and responsive to disturbances around them. This was at a time when the limb buds could not be detected and when the external gills were evident only under close scrutiny.

Two times we found adult female salamanders in the chambers with the egg clusters. The other two egg clutches seemingly had no attendant adult, but our method of going through a log was such that we could easily have alarmed any attendant animal well before we found the eggs, allowing time for the adult to move away from the eggs. We presume that incubation, so-called, in *A. hardii* is similar to that found in other plethodontids (see, for example, Gordon, 1952:683). Our findings on the conditions of the stomachs of these attendant adults have been outlined above ("Food and Foraging"). Our limited data suggest that only females are found in chambers with eggs.

Summary

The montane relict plethodontid *Aneides hardii* was studied in the field and laboratory in 1956-1958. Food items detected in a small sample of stomachs are listed tabularly. Two roundworms were found to parasitize the guts of the salamanders; the parasitism looks to be benign. Subterranean winter inactivity is thought to be an integral part of the salamanders' lives, and is suggested in part

by the life cycles of the worms. Summer activity appears to occur at the ground surface in logs and talus, and underground; the latter site is suggested by certain ratios obtained in the samples, showing adults to outnumber young and males to outnumber females. The season for egg deposition seems to be in July and August. Clutch-size is lower than for any other plethodontid on record. "Incubation" of eggs apparently parallels that characteristic of other plethodontids.

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Transmitted May 11, 1959.

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Vol. 10, No. 9, pp. 587-598, 2 figs.
May 2, 1960

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UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
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28-2494

A New Subspecies of Lizard, Cnemidophorus sacki, from Michoacán, México

BY

WILLIAM E. DUELLMAN

The systematic status of the populations of lizards assignable to *Cnemidophorus sacki* in western México (Sonora southward to Jalisco) has been reviewed in detail by Zweifel (1959, Bull. Amer. Mus. Nat. Hist., 117 (2):57-116), who stated that the use of the specific name *sacki* for the western populations rests upon a reasonable, but as yet unproved, assumption that intergradation occurs. Although Zweifel examined specimens of the nominal subspecies from the upper Balsas Basin, he did not study specimens from the intervening area—the Tepalcatepec Valley in Michoacán.

Field studies and the examination of large series of preserved specimens of *Cnemidophorus* from the Tepalcatapec Valley show the presence of *Cnemidophorus sacki* in the region between the ranges of *C. sacki sacki* in the upper Balsas Basin and *C. sacki occidentalis* in Jalisco and southern Nayarit. Furthermore, the populations of *sacki* inhabiting the Tepalcatepec Valley have characters of scutellation and coloration that distinguish them from other described subspecies of *sacki*. In recognition of the important contributions to the systematics of the genus *Cnemidophorus* made by Dr. Richard G. Zweifel, I propose that the subspecies of *Cnemidophorus sacki* in the Tepalcatepec Valley be named as follows:

Cnemidophorus sacki zweifeli new subspecies

Holotype.—University of Michigan Museum of Zoology No. 119542, from Capirio, Michoacán, México (185 meters), an adult male, one of a series collected on June 13, 1958, by William E. Duellman, Jerome B. Tulecke, and John Wellman. Original number WED 12310.

Paratopotypes.—UMMZ Nos. 119536-119541 and 119543-119550.

Diagnosis.—A race of *Cnemidophorus sacki* characterized by large size (more than 130 mm. snout-vent length in males), approximately 106 dorsal granules around the midbody, about 41 femoral pores, and a dorsal color-pattern in adult males consisting of lateral and dorsolateral rows of spots, paravertebral rows fused with middorsal light green area at least anteriorly, and pink throat having a median light blue spot or transverse band.

Description of Holotype.—Snout-vent length, 128 mm.; tail length, 252 mm.; tail/body ratio, 1.97; scutellation typical of *sacki*—four supraoculars, enlarged postantebrachials, and enlarged mesoptychials; 107 granules around midbody (excluding enlarged ventrals); 45 femoral pores; three enlarged preanal scales; supraorbital semicircle-series extending anteriorly to posterior edge of frontal (Fig. 1).

Top of head and nape dusty brown; tip of rostral and lateral edges of superciliaries dark cream-color; upper labials and sides of head anterior to

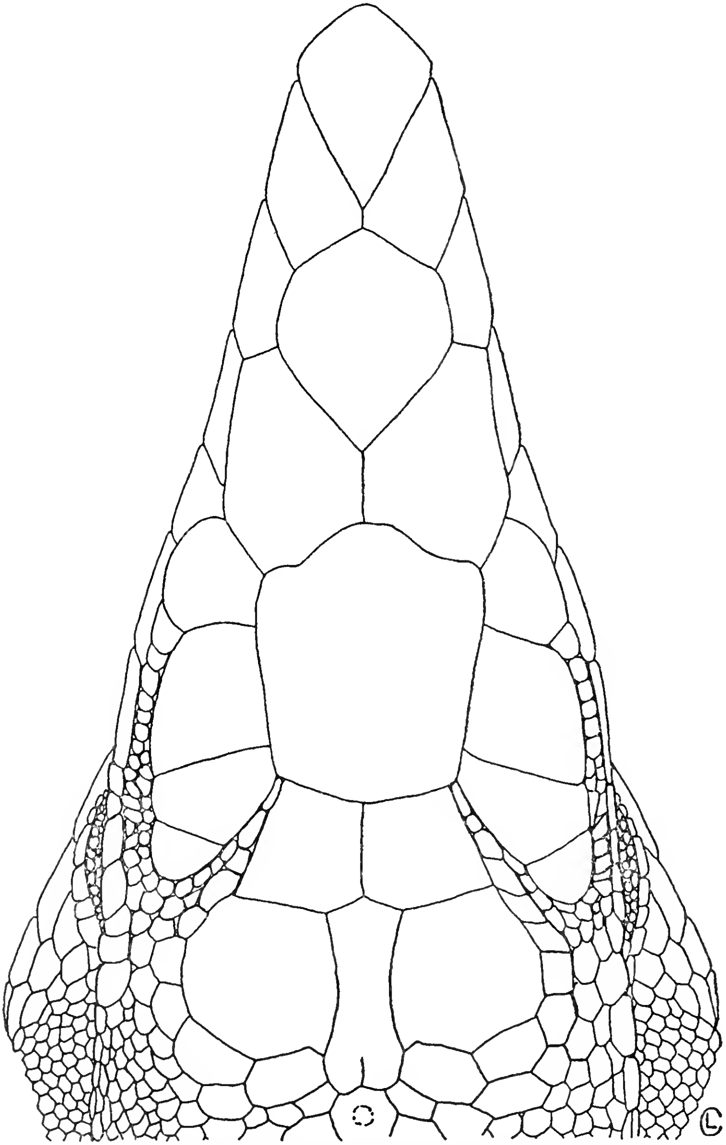

Fig. 1. Top view of the head of the holotype of *Cnemidophorus sacki zweifeli* (UMMZ 119542) showing scutellation. × 5.

eyes cream-color, mottled with blue; lower labials and postocular region pale blue; mental, postmental, and sublabials cream-color. Upper surfaces of forelimbs dull bluish gray, spotted with pale greenish yellow; dorsal surfaces of proximal one-fourth of tail light brownish gray turning to pale orange-brown posteriorly; lateral surfaces of tail bluish gray anteriorly and creamy brown posteriorly. Nuchal region light bluish gray; flanks dark gray; dorsal ground-color dark brown, somewhat paler posteriorly. Body having a row of cream-colored spots in place of a lateral stripe, and another row in place of dorsolateral stripe; dorsally, large diffuse tan or light green spots partially fused and tending to form irregular transverse markings. Chin to posterior end of sublabials pale pink, bordered posteriorly by bluish white area, and then pink. Mesoptychials, under surfaces of hind limbs, and belly cream-colored; anterior edges of belly scales dark blue; lateral two rows of ventrals on posterior two-thirds of body dark blue having light blue or cream-colored spots. Under surfaces of forelimbs bluish cream; ventral surface of tail cream-colored.

Variation in Size and Scutellation.—The largest male has a snout-vent length of 132 mm., the largest female, 114 mm., and the smallest juvenile, 34 mm. The number of dorsal granules at the midbody varies from 91 to 117 (106.2 ± 0.43); the ratio of the number of granules between the paravertebral stripes to the number of granules around the body (PV/GAB) varies from 0.064 to 0.157 (0.097 ± 0.007); the number of femoral pores varies from 32 to 49 (41.1 ± 0.20). Usually there are only three enlarged preanals, but 18 specimens have a somewhat enlarged scale anterior to the normal complement of three. In 15 specimens the supraorbital semicircle-series terminate short of the posterior edge of the frontal; in the others the series reach the frontal.

Variation in Coloration.—The coloration of juveniles and subadults varies little; large adults vary considerably especially in the amount of diffusion of the light green middorsal area. In some individuals the vertebral pale area does not include the paravertebral spots; in other individuals the pale area includes not only the paravertebral rows, but, at least anteriorly, the dorsolateral rows. In large males of about equal size (and collected at the same time) there is considerable variation in the amount of blue on the belly. In a few of the males the belly is white with only the anterior edge of each scale blue; in some only the lateral rows of ventrals on the posterior two-thirds of the body are blue; in others all of the posterior two-thirds of the belly is blue.

Ontogenetic Change in Color Pattern.—The metamorphosis of color pattern in *Cnemidophorus sacki zweifeli* results in the dorsal ground-color becoming paler with age, the replacement of the stripes by spots, and finally in large males the suffusion of these spots.

A single hatchling (UMMZ 114732) is available; this specimen has a prominent umbilical scar and a snout-vent length of 34 mm. The top of the head is olive brown; the dorsal surfaces of the limbs are dark brown with cream mottling; the dorsal ground-color is brownish black; this is paler on the lower flanks. The lateral and dorsolateral stripes are cream-colored; the paravertebral stripes are white. There is a faint, diffuse vertebral stripe anteriorly (Fig. 2 A). The throat and undersides of the limbs and tail are cream-colored; the belly is bluish white. In life the stripes were pale yellowish green, and the tip of the tail was pink.

In larger individuals the dorsal ground color is dark brown; the lower flanks are grayish tan. Light brown diffuse spots are present in the lateral and dorsolateral dark fields. The tan vertebral stripe is diffuse and nearly fills the paravertebral dark fields; the paravertebral stripes are faint posteriorly; throughout their length they are scalloped—the beginning of their fragmentation into spots (Fig. 2 B).

In subadults (± 80 mm. snout-vent length) the paravertebral stripes are fragmented into spots posteriorly. Also, the dorsolateral stripes in some individuals are fragmented posteriorly. The dorsolateral dark fields are somewhat paler than the lateral dark fields. Cream-colored spots are present on the flanks. The mottling on the thighs tends towards the formation of light spots (Fig. 2 C).

In small adults (± 100 mm. snout-vent length) the paravertebral stripes are entirely fragmented into spots. The lateral and dorsolateral stripes are broken into spots posteriorly. The middorsal pale area (formed by the suffusion of the vertebral stripe) and paravertebral and dorsolateral rows of spots are pale green. The cream-colored spots on the flanks are expanded to form vertical bars (Fig. 2 D).

Large adult males (± 120 mm. snout-vent length) have all of the stripes fragmented into spots. The diffuse middorsal area is expanded and encloses the paravertebral rows of spots. The pale spots present in the dark fields in smaller individuals are either absent or fused with spots resulting from the fragmentation of the stripes (Fig. 2 E).

Sexual dimorphism.—Males attain a larger size (known maximum snout-vent length of 132 mm., as compared with 114 mm. in females). Males have larger but not more numerous, femoral pores, blue bellies, and pink and blue throats, whereas females are unicolor creamy white ventrally. The more nearly complete metamorphosis of color pattern exhibited by adult males probably is correlated with their large adult size. Large females retain complete lateral and dorsolateral stripes. The jowls of breeding males are swollen.

Geographic variation.—No noticeable geographic variation in this subspecies is evident in the series from the Tepalcatepec Valley. However, lizards from eastern Michoacán (Chinapa, 6

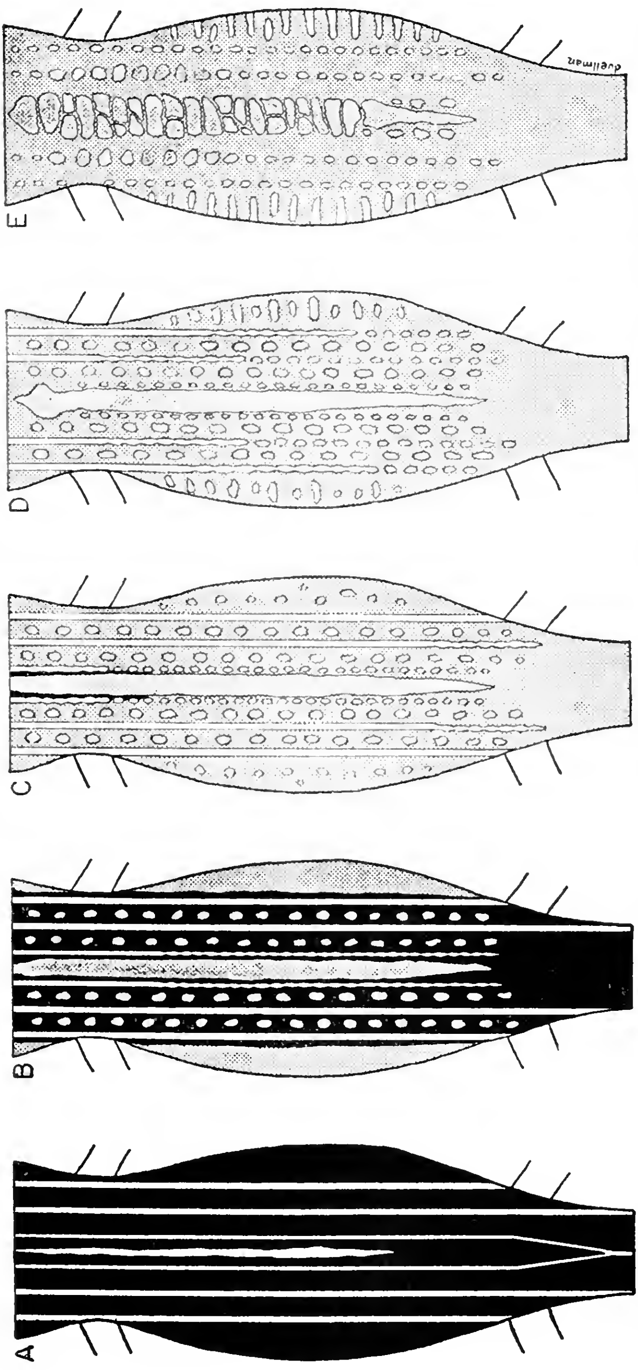

FIG. 2. Diagrammatic representation of ontogenetic change in color pattern in *Cnemidophorus sacki zweifeli:* A— hatchling, 34 mm. snout-vent length; B—juvenile, 55 mm. snout-vent length; C—subadult male, 80 mm. snout-vent length; D—small adult male, 100 mm. snout-vent length; E—large adult male, 120 mm. snout-vent length.

km. N of Tafetan, 6 km. S of Tzitzio, and 19 km. S of Tzitzio) differ slightly from those from the Tepalcatepec Valley; the eastern specimens have fewer dorsal granules and femoral pores, and a higher ratio of dorsal granules between the paravertebral stripes to the number of granules around the body (see Tables 1-3). No large adult males are present in the eastern series; the subadults and small adult males have color patterns like lizards of similar size from the Tepalcatepec Valley. The largest male from the east has a snout-vent length of 110 mm., rows of pale spots, and no trace of brown and tan cross-bars. Specimens of *Cnemidophorus sacki sacki* of equal size from Guerrero, Morelos, and Puebla in the upper Balsas Basin have a tan dorsum with dark brown cross-bars. The localities in eastern Michoacán are intermediate geographically between the Tepalcatepec Valley and the known range of the nominal subspecies in the upper Balsas Basin. In characters of scutellation specimens from the east are intermediate between *C. sacki sacki* and *C. sacki zweifeli* in the Tepalcatepec Valley. However, in coloration the lizards from the east are like those from the Tepalcatepec Valley, but differ distinctly from the nominal subspecies. Therefore, the eastern series is referred to the subspecies *C. sacki zweifeli.*

Comparisons.—Four other species of *Cnemidophorus* occur in the Tepalcatepec Valley with *Cnemidophorus sacki zweifeli.* Of these, *C. calidipes* has a maximum snout-vent length of 79 mm., 66 to 86 dorsal granules, and a light brown dorsum with pale blue spots and vertical bars; *C. communis communis* has a maximum snout-vent length of 135 mm., 105 to 144 dorsal granules, and a greenish tan dorsum with yellow spots; *C. deppei infernalis* has a maximum snout-vent length of 84 mm., 91 to 120 dorsal granules, and a striped pattern throughout life; and *C. lineatissimus exoristus* has a maximum snout-vent length of 98 mm., 108 to 135 dorsal granules, and a middorsal yellow stripe and vertical bars on the flanks. Both *calidipes* and *communis* are like *sacki* in possessing four enlarged supraoculars and enlarged postantebrachials, whereas *deppei* and *lineatissimus* have three enlarged supraoculars and granular postantebrachials. Juveniles of *calidipes* and *sacki* are alike in coloration but different in the extent of the supraorbital semicircle-series. In *calidipes* the supraorbital semicircle-series usually are complete, whereas in *sacki* the series never extended anterior to the posterior edge of the frontal.

TABLE 1.—VARIATION IN THE NUMBER OF DORSAL GRANULES IN THREE SUBSPECIES OF CNEMIDOPHORUS SACKI

POPULATION	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation
sacki sacki						
Entire Sample	106	88–105	96.3	4.16	0.40	3.92
Puebla: Tehuitzingo	22	88–103	95.1	4.18	0.89	4.39
Guerrero: Chilpancingo	23	90–105	95.8	3.86	0.80	4.02
Guerrero: Mexcala	22	90–102	96.5	3.56	0.76	3.69
Morelos	39	89–105	97.2	4.56	0.73	4.69
sacki zweifeli						
Entire Sample	191	91–117	106.2	5.98	0.43	3.13
Michoacán: Tafetan	21	91–116	101.4	8.04	1.75	7.92
Michoacán: Apatzingán	170	95–117	106.8	5.42	1.32	3.19
*sacki occidentalis**	62	97–118	106.3	4.72	0.60	7.61

* Data for *C. sacki occidentalis* in Tables 1-3 are from Zweifel (1959, Bull. Amer. Mus. Nat. Hist., 117: tables 1-3).

TABLE 2.—VARIATION IN THE NUMBER OF FEMORAL PORES IN THREE SUBSPECIES OF CNEMIDOPHORUS SACKI

POPULATION	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation
sacki sacki						
Entire Sample	106	32–44	36.2	2.42	0.25	2.28
Puebla: Tehuitzingo	22	33–41	36.7	2.36	0.50	6.43
Guerrero: Chilpancingo	23	32–39	35.7	2.15	0.45	6.02
Guerrero: Mexcala	22	33–44	37.5	2.59	0.55	6.91
Morelos	39	32–40	35.4	2.19	0.35	6.18
sacki zweifeli						
Entire Sample	189	32–49	41.1	2.77	0.20	1.46
Michoacán: Tafetan	19	33–43	38.1	2.61	0.60	6.85
Michoacán: Apatzingán	170	32–49	41.4	2.58	0.62	1.52
sacki occidentalis	67	32–45	38.8	2.46	0.30	3.67

TABLE 3.—RATIO OF NUMBER OF GRANULES SEPARATING PARAVERTEBRAL STRIPES TO GRANULES AROUND MIDBODY (PV/GAB) IN THREE SUBSPECIES OF CNEMIDOPHORUS SACKI

POPULATION	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation
sacki sacki						
Entire Sample........	72	0.101–0.205	0.154	0.052	0.006	0.073
Puebla: Tehuitzingo...	12	0.140–0.205	0.169	0.052	0.015	0.433
Guerrero: Chilpancingo	16	0.120–0.192	0.157	0.021	0.005	0.131
Guerrero: Mexcala....	21	0.142–0.180	0.159	0.031	0.007	0.147
Morelos..............	23	0.101–0.180	0.137	0.023	0.005	0.100
sacki zweifeli						
Entire Sample........	105	0.064–0.157	0.097	0.070	0.007	0.067
Michoacán: Tafetan...	21	0.103–0.157	0.128	0.039	0.009	0.186
Michoacán: Apatzingán	84	0.064–0.126	0.089	0.051	0.005	0.060
sacki occidentalis.........	50	0.086–0.183	0.130	0.021	0.003	0.042

From the geographically adjacent populations of *sacki (sacki* and *occidentalis), zweifeli* differs in coloration and scutellation (see Tables I-III). *Cnemidophorus sacki sacki* has a dorsal pattern in adult males of dark brown cross-bars on a tan ground-color. Both *occidentalis* and *zweifeli* have variable, diffuse color patterns in large adults, but *zweifeli* differs from *occidentalis* in having a blue spot on the pink throat.

Ecology.—In the arid Tepalcatepec Valley *Cnemidophorus sacki zweifeli* lives at elevations of 160 to 1300 meters. In the lower parts of the valley the lizards live primarily in open scrub forests, characterized by deciduous trees offering only partial shade from the sun, especially during the prolonged dry season. Common trees in this scrub forest are *Acacia cymbispina, Cercidium plurifoliolatum, Mimosa distachya,* and *Prosopis juliflora.*

During the dry season (November through May) adult males apparently aestivate; several large series collected in the winter include only subadults and females. This absence of males is corroborated by personal observations in the Tepalcatepec Valley in April and May. In the summer rainy season the lizards are active in the morning and again in the late afternoon; only *Cnemidophorus calidipes* is active during the heat of the midday. In some areas of the scrub forest *Cnemidophorus sacki zweifeli* is found in association with *Cnemidophorus communis communis.* Throughout the scrub forest *C. sacki zweifeli* occurs with *C. deppei infernalis.* In some of the more dense scrub forest, where *C. sacki zweifeli* is not so abundant as in the more open forest, it has been taken with *C. lineatissimus exoristus.* In the open *Acacia-Cercidium* associations on the valley floor *C. sacki zweifeli* occurs with *C. calidipes.*

This subspecies is not restricted to the scrub forest. On the lower slopes of the Cordillera Volcanica in Michoacán *C. sacki zweifeli* has been collected in open pine-oak forest near Zirimicuaro and Ziracuaretiro.

Distribution.—Cnemidophorus sacki zweifeli inhabits the valley of the Río Tepalcatepec in Michoacán and probably extreme southwestern Jalisco, and the western part of the Balsas Basin in Michoacán. No specimens have been seen from extreme western Guerrero, but *C. s. zweifeli* may occur there.

Specimens examined.—Catalogue numbers are preceded by abbreviations of the name of the institution as listed in the acknowledgements.

Cnemidophorus sacki occidentalis, 22 specimens, as follows: *Jalisco:* 8 km. E of Ameca, UMMZ 102045; 7 km. SE of Ameca, UMMZ 102046; Autlán, UMMZ 102044, 102219-21; 7 km. ESE of El Arenal, UMMZ 114736 (2); San Gabriel, UMMZ 102040, 102042-3. *Michoacán:* 2 km. ESE of Jiquilpan, UMMZ 117557 (3). *Nayarit:* Ixtlán del Río, UMMZ 104747; San José de la Conde, UMMZ 102047 (4); 5 km. N of Santa Isabel, UMMZ 102048-50.

Cnemidophorus sacki sacki, 108 specimens, as follows: *Guerrero:* Chilpancingo, UMMZ 72426 (8), 73937 (7), 88422 (4); 8 km. W of Chilpancingo, UMMZ 119144 (4); 5 km. N of Iguala, UMMZ 114712 (11); 15 km. N of Iguala, UMMZ 99039; Mexcala, UMMZ 114711 (10); 8 km. S of Taxco, UMMZ 114709 (2). *Morelos:* Amacuzac, UMMZ 114716; 3 km. S of Cuautla, UMMZ 99031 (9), 99917 (11); Río Cuautla, UMMZ 99038 (6); 5 km. S of Temixco, UMMZ 114718 (12); *Puebla:* 5 km. SE of Izúcar de Matamoros, UMMZ 112650 (4); 13 km. SE of Izúcar de Matamoros, UMMZ 117497 (2); 3 km. NW of Tehuitzingo, UMMZ 114714 (10); 1 km. N of Teyuca, UMMZ 114713 (6).

Cnemidophorus sacki zweifeli, 207 specimens, as follows: *Michoacán:* Apatzingán, CNHM 36966-8, 38969, 38971 (18), 38972 (50), UIMNH 36772-7, USNM 135967-8, 135970, 135972-3; 4 km. E of Apatzingán, UMMZ 85412; 6.5 km. E of Apatzingán, UMMZ 114731 (5); 5 km. W of Apatzingán, KU 29289-90, 29293-7; 10 km. W of Apatzingán, UMMZ 114730 (4); 12.3 km. S of Apatzingán, UMMZ 112647; 16 km. S of Apatzingán, KU 29298; 14 km. SSW of Apatzingán, KU 29735, 29746, 29750-2; 10 km. W of Buenavista, UMMZ 114719 (3); Capirio, UMMZ 112643, 114722 (2), 114733, 119536-50; 4 km. N of Capirio, UMMZ 112644 (3), 112645; 5.6 km. N of Capirio, UMMZ 114732; 2 km. S of Charapendo, UMMZ 112639 (12); Chinapa, UMMZ 119556 (2); Jazmin, UMMZ 114725 (2); between La Playa and Volcán Jorullo, UMMZ 104748 (2); Limoncito, UMMZ 119552 (3); 14 km. S of Lombardia, KU 29299-301, 29303, 29305-11; 6 km. SW of Nueva Italia, UMMZ 112640 (2); 2.7 km. S of Nueva Italia, UMMZ 112641 (4); 5 km. N of Nueva Italia, UMMZ 114721; Río Marquez, 10 km. S of Lombardia, UMMZ 112642, 112646; Río Marquez, 13 km. SE of Nueva

Italia, UMMZ 114726; 6 km. N of Tafetan, UMMZ 119555 (18); 14.5 km. E of Tepalcatepec, UMMZ 114720 (2); 6 km. S of Tzitzio, UMMZ 99199, 99200 (2); 19 km. S of Tzitzio, UMMZ 99154; Volcán Jorullo, UMMZ 104449 (4), 104750; Ziracuaretiro, UMMZ 114724; 3 km. NW of Zirimicuaro, UMMZ 114723.

Acknowledgments.—For the loan of specimens under their care I am indebted to Doris M. Cochran, United States National Museum (USNM); Norman Hartweg, University of Michigan Museum of Zoology (UMMZ); Robert F. Inger, Chicago Natural History Museum (CNHM); and Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH). I thank Ann S. Duellman, Richard E. Etheridge, Fred G. Thompson, Jerome B. Tulecke, and John Wellman for their assistance in the field, Lorna Cordonnier for the drawing reproduced as Figure 1, and Richard G. Zweifel for helpful suggestions and criticism. Field work in México was made possible by grants from the Penrose Fund of the American Philosophical Society and the Bache Fund of the National Academy of Sciences in co-operation with the Museum of Zoology of the University of Michigan.

Transmitted February 2, 1960.

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28-2494

University of Kansas Publications
Museum of Natural History

Vol. 10, No. 10, pp. 599-610, 1 pl., 1 fig.
May 2, 1960

A Taxonomic Study of the Middle American Snake, Pituophis deppei

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1960

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Volume 10, No. 10, pp. 599-610, 1 pl., 1 fig.
Published May 2, 1960

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1960
28-2493

PLATE 45

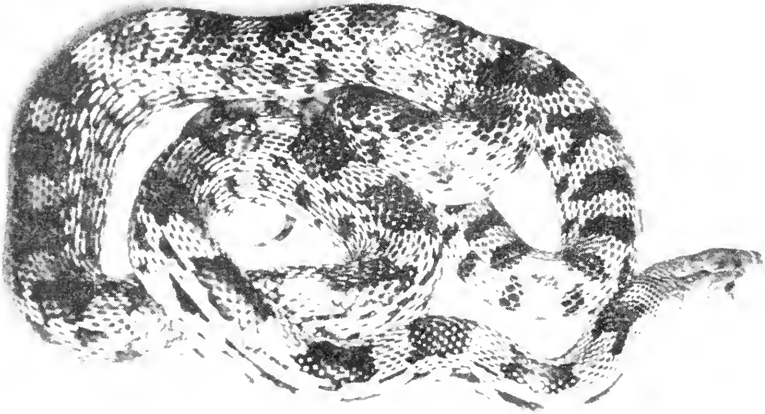

FIG. 1. *Pituophis deppei deppei* from Cumbres de Acultzingo, Veracruz, UMMZ 114596. Approx. ½ natural size.

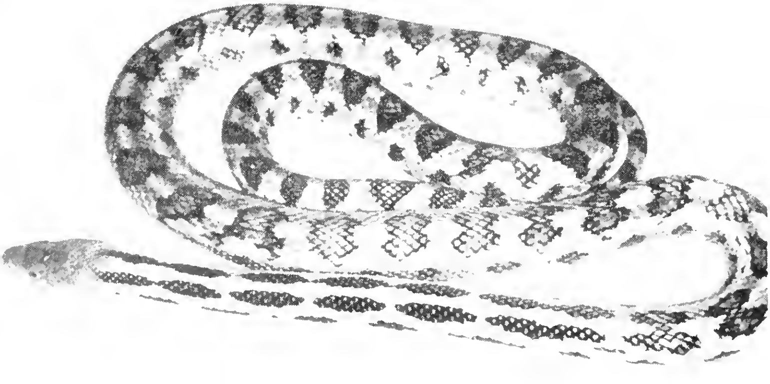

FIG. 2. *Pituophis lineaticollis lineaticollis* from Dos Aguas, Michoacán, UMMZ 119567. Approx. ⅓ natural size.

A Taxonomic Study of the Middle American Snake, Pituophis deppei

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WILLIAM E. DUELLMAN

INTRODUCTION

As a part of a study of the herpetofauna of the Mexican state of Michoacán an attempt was made to ascertain the interspecific and intraspecific relationships of the various populations of *Pituophis* there. Field work in Michoacán revealed that two supposed subspecies of *Pituophis deppei* were sympatric. This discovery led to the examination of all available (124) museum specimens of these snakes.

I am grateful to the following persons who permitted me to examine specimens in their care: Charles M. Bogert, American Museum of Natural History (AMNH); Doris M. Cochran, United States National Museum (USNM); Norman Hartweg, University of Michigan Museum of Zoology (UMMZ); Robert F. Inger, Chicago Natural History Museum (CNHM); Arthur Loveridge, Museum of Comparative Zoology (MCZ); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); and Edward H. Taylor, E. H. Taylor—H. M. Smith collection (EHT-HMS). Specimens in the accounts of the species are listed after the abbreviations of the institutions given in parentheses above.

HISTORICAL REVIEW

Duméril (1853:453) described *Elaphis deppei* from a specimen in the Leiden Museum from "Mexico." This specimen, according to the type description, has 233 ventrals and 67 caudals. In 1863 Jan described *Pituophis deppei* var. *pholidostictus,* also with "Mexico" as the type locality. Subsequent authors (see synonymy of *P. deppei deppei* in Stull, 1940: 25) have treated *pholidostictus* as a synonym of *deppei.* Smith and Taylor (1950: 334) restricted the type localities of *deppei* and *pholidostictus* to San Juan Teotihuacán, México. Cope (1860: 369) described *Arizona jani* on the basis of a specimen in the United States National Museum from Buena Vista, Coahuila. Stull (1932: 2, 1940: 42), Smith (1944: 145) and Smith and Taylor (1945: 107) considered *jani* as a northern subspecies of *Pituophis deppei.* *Arizona lineaticollis* was described by Cope (1861: 300); the type, which originally was in the Academy of Natural Sciences of Philadelphia and is now lost, was said to have come from Jalapa, Veracruz. This locality probably is in error. Smith (1943: 460) placed *lineaticollis* as a southern subspecies of *deppei*. Schmidt and Shannon (1947: 79) described *Pituophis deppei brevilineata* on the basis of five specimens from Tancítaro, Michoacán, and Stuart (1954: 172) described *Pituophis deppei gibsoni* from seven specimens from Departamento Chimaltenango, Guatemala. Thus, at present five subspecies of *Pituophis deppei* are recognized.

CHARACTERS STUDIED

Snakes currently assigned to *Pituophis deppei* differ from other members of the genus by possessing two instead of four prefrontal plates. The subspecies of *P. deppei* have been defined on characters of coloration and scutellation.

Scutellation.—The only scale characters utilized in the present study are the numbers of ventrals and caudals. The number of ventrals varies in the total sample from 210 to 246 (Table 1); usually the variation in one locality is no more than 15. Number of caudals varies from 52 to 72. There is slight sexual dimorphism in the number of ventrals and somewhat greater differences in the number of caudals.

TABLE 1.—VARIATION IN THE NUMBERS OF VENTRALS AND CAUDALS IN FOUR SUBSPECIES OF PITUOPHIS.

SUBSPECIES	Ventrals		Caudals	
	Range	Mean	Range	Mean
deppei deppei				
34 ♂♂	210–231	220.4	53–69	61.5
16 ♀♀	209–232	218.2	52–61	57.2
deppei jani				
12 ♂♂	215–235	225.1	56–68	62.6
3 ♀♀	228–231	229.0	52–60	56.0
lineaticollis lineaticollis				
13 ♂♂	231–258	239.5	54–72	64.9
9 ♀♀	229–249	241.3	55–68	60.6
lineaticollis gibsoni				
2 ♂♂	234	234.0	61–65	63.0
4 ♀♀	241–246	243.7	57–63	59.0

Coloration.—The dorsal ground color is tan or straw; the dorsal pattern consists basically of dark middorsal blotches and dark lateral intercalary spots. Number of blotches, color of blotches posteriorly, width of pale interspaces between anterior blotches, and color of lateral intercalary spots vary considerably geographically. In some populations *(lineaticollis* and *gibsoni)* the anterior blotches are divided medially forming either a pair of dark stripes on the anterior part of the body or a series of paired spots. Details of coloration are described in the following accounts.

ACCOUNTS OF THE SPECIES AND SUBSPECIES

Study of *Pituophis deppei (auctorum)* revealed the presence of sympatric populations of two distinct species of *Pituophis* differing

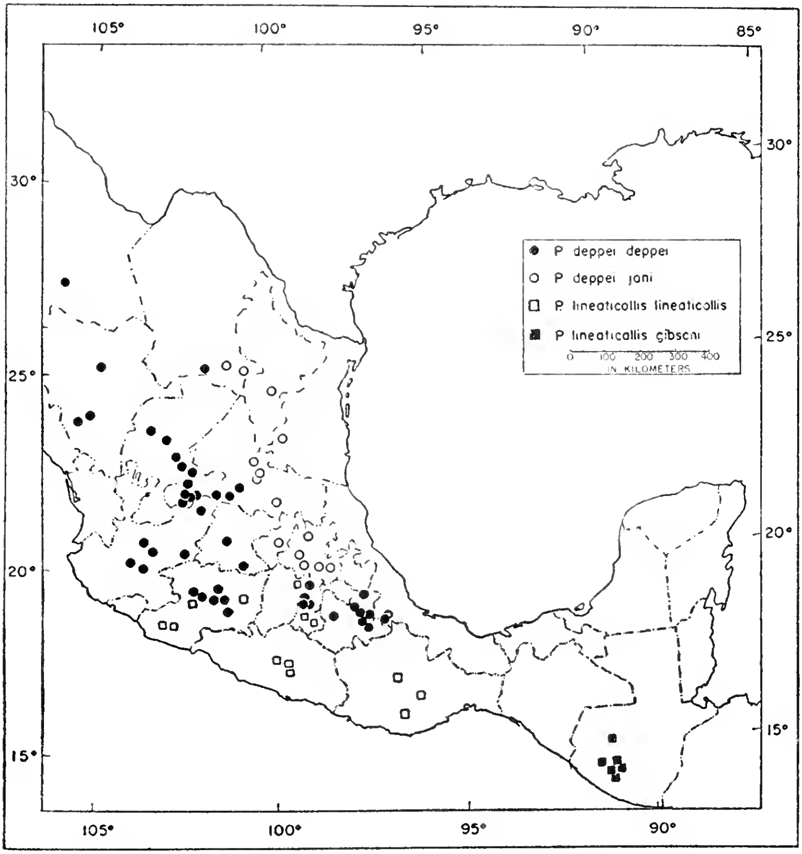

FIG. 1. México and Guatemala showing the distribution of the subspecies of *Pituophis deppei* and *P. lineaticollis.*

from each other in scutellation and coloration. The nomenclature resulting from the required rearrangement necessitates the recognition of 1) *deppei* as a species, 2) *jani* as a subspecies of *deppei,* 3) *lineaticollis* (with *brevilineata* as a synonym) as a species distinct from *deppei,* and 4) *gibsoni* as a subspecies of *lineaticollis.* Known geographic distributions of these named taxa are shown in Figure 1.

Pituophis deppei deppei Duméril

Elaphis deppei Duméril, Mem. Acad. Inst. France, vol. 23, p. 453, 1853; Duméril and Bibron, Erpétologie générale, vol. 7. p. 268, February 25, 1854.

Pituophis deppei, Jan, Elenco sistematico degli ofidi, p. 59, 1863; Günther, Biologia Centrali-Americana, Reptilia, p. 124, February, 1894.

Elaphis pleurostictus Duméril, Mem. Acad. Inst. France, vol. 23, p. 453, 1853 [Type.—Museum d'Histoire Naturelle Paris, No. 6616; type locality —"Monte Video" (restricted to San Juan Teotihuacán, México, by Smith and Taylor, 1950: 334)].

Pituophis pleurostictus, Jan, Elenco sistematico degli ofidi, p. 59, 1863.

Pituophis deppei, var. *pholidostictus* Jan, Elenco sistematico degli ofidi, p. 59, 1863 [Type.—Zoologisches Museum Berlin, No. 1738; type locality.—"Mexico" (restricted to San Juan Teotihuacán, México, by Smith and Taylor, 1950: 334)].

Pituophis deppei deppei, Stull, Occas. Papers Mus. Zool. Univ. Michigan, no. 250, p. 1, October 12, 1932; Bull. U. S. Natl. Mus. 175, p. 25, April 23, 1940; Smith and Taylor, U. S. Natl. Mus., no. 187, p. 107, 1945.

Type.—Rijkmuseum van Natuurlijke Histoire, Leiden, No. ???, obtained by Ferdinand Deppe. The type locality was originally given as "Mexico"; this was restricted to San Juan Teotihuacán, state of México, by Smith and Taylor (1950: 334).

Diagnosis.—This subspecies is characterized by the presence of solid body-blotches and lateral intercalary spots, dorsal interspaces less than five scales in length, and the absence of paired stripes or rows of blotches, on the anterior part of the body. There are 209 to 232 ventrals and 52 to 62 caudals. The body-blotches number 27 to 49. In adults the anterior and posterior body-blotches are black; the lateral intercalary spots are solid black. In many individuals black dashes connect the adjacent corners of the dorsal body-blotches (Pl. 45, Fig. 1). In juveniles the anterior, dorsal body-blotches are black, whereas those at the midbody and posteriorly are brown.

Variation.—Geographically, scutellation varies only slightly. Comparison of specimens from the northern part of the Mexican Plateau (Chihuahua, Coahuila, and Durango—5 specimens), the central part of the plateau (Aguascalientes, San Luis Potosí, and Zacatecas—13 specimens), the southern part of the plateau (Guanajuato, Jalisco, México, and Michoacán—18 specimens), and Puebla and southern Veracruz (12 specimens) shows the average number of ventrals for these samples to be, respectively, 221.6, 216.7, 221.3, and 220.0. The average number of dorsal body-blotches for the same samples are, respectively, 36.6, 37.7, 38.4, and 34.6. Only in the southernmost sample is there a noticeable difference in the number of blotches.

The specimen from Párajo Verde, Veracruz, was considered to be an intergrade between *P. deppei* and *P. lineaticollis* by Smith (1943:461), who stated that, although the snake had 231 ventrals and dark lateral streaks as does *deppei*, it had light-centered dorsal blotches and stripes on the neck as does *lineaticollis*. This specimen (USNM 110892) has a high number of ventrals for *deppei*; one from Jalisco has 232, and one each from Guanajuato and Veracruz have 229. The blotches posteriorly are lighter than those anteriorly and are slightly lighter in the center than at the periphery. Two anterior blotches are divided medially and narrowly connected by black streaks. Although these are somewhat suggestive of the pattern of *lineaticollis*, they are more nearly like that of *deppei*. Four other specimens from the same area are typically *deppei*. There is some doubt as to the actual provenance of the snake stated to have come from Párajo Verde, for, according to Smith (1943: 460), the snake had been tied to a truck and dragged halfway down the slopes of the Cumbres de Acultzingo, where he found it. He surmised that it probably was dragged no farther than the settlement, Párajo Verde, at the Cumbres de Acultzingo.

Fugler and Webb (1956: 171) commented on the uniformly brown dorsum of a specimen (KU 39564) from 16 miles east and 18 miles north of Ocampo, Coahuila. It has a higher number of ventrals (242) and caudals (88) than is known for *deppei*. It is, without a doubt, a *Pituophis*. It is not *Pituophis catenifer*, as attested to by the presence of only two prefrontals. The high number of ventrals and caudals, together with the uniform dark brown dorsum, provide a combination of characters indicating that this specimen may represent an undescribed species in the *deppei* group of *Pituophis*.

Distribution.—Southern Chihuahua and southern Coahuila southward on the western and central parts of the Mexican Plateau to the Valley of México and to southeastern Puebla and adjacent Veracruz.

Specimens examined.—Total of 63, as follows: *Aguascalientes*: 16 km. N of Aguascalientes, UIMNH 27149; 17 km. E of Aguascalientes, UIMNH 36222; 5 km. SW of Aguascalientes, KU 29495; Cavillito, UIMNH 28134; 11 km. N of Rincon de Romos, UIMNH 40359-60; 2 km. N of San Francisco de los Romos, UIMNH 27569. *Chihuahua*: USNM 8321 (2 specimens); Semachique, CNHM 11825. *Coahuila*: Castanuelas, MCZ 407. *Distrito Federal:* Lago Xochimilco, UIMNH 18709; Pedregal, UMMZ 99790. *Durango*: Coyotes, CNHM 1497; Hacienda Magdalena, USNM 46365; Llano Grande, UMMZ 113634. *Guanajuato*: USNM 16442; Acambaro, KU 45003;

Irapuato, UIMNH 35055. *Jalisco*: Atemajac, USNM 46385; Guadalajara, USNM 24969; 5 km. SE of Guadalajara, KU 29508; Jamay, AMNH 19848-9, 19851-2; 3 km. WNW of Lagos de Moreno, KU 27727; 5 km. NW of Sayula, UMMZ 101933. *México:* Atzocozlco, AMNH 19850; Chalco, USNM 110889; San Juan Teotihuacán, EHT-HMS 5378, 5383, MCZ 16051. *Michoacán:* 6 km. E of Carapan, AMNH 69940; 3 km. W of Carapan, UMMZ 114598; 14 km. W of Morelia, UMMZ 104969; Tacambaro, USNM 46557; Tacícuaro, USNM 110888; 11 km. W of Zacapu, UMMZ 104968. *Puebla*: Alseseca, UIMNH 36221; Atlixco, USNM 46433; Puebla, AMNH 19856; 30 km. N of Puebla, USNM 110887; Tecamachalco, UMMZ 88688; 16 km. SSE of Tecamachalco, UMMZ 114597; Tehuacan, UMMZ 88687; 22 km. N of Tehuacan, EHT-HMS 5377. *San Luis Potosí:* USNM 46554; 26 km. SW of San Luis Potosí, UIMNH 28133. *Veracruz*: 3 km. W of Acultzingo, KU 23978; Cumbres de Acultzingo, UIMNH 36224, 36226, UMMZ 114596; Párajo Verde, USNM 110892; questionably from Potrero Viejo, UMMZ 89358-9. *Zacatecas*: 16 km. E of Somberete, UIMNH 27147; 1 km. SW of Tiburcio, KU 33599; 3 km. ESE of Troncoso, KU 29494; 10 km. W of Villa de Arriaga (San Luis Potosí), UIMNH 27151; 24 km. NW of Zacatecas, UIMNH 6393; 13 km. SE of Zacatecas, UIMNH 27148; 26 km. SE of Zacatecas, UIMNH 27568.

Pituophis deppei jani Cope

Arizona jani Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 369, 1860.

Pituophis deppei jani, Stull, Occas. Papers Mus. Zool. Univ. Michigan, no. 250, p. 2, October 12, 1932, Bull. U. S. Natl. Mus., no. 175, p. 42, April 23, 1940; Smith, Zool. Ser. Field Mus. Nat. Hist., vol. 29, p. 145, February 29, 1944; Smith and Taylor, Bull. U. S. Natl. Mus., no. 187, p. 107, 1940.

Type.—United States National Museum, No. 1522, from Buena Vista, Coahuila, obtained by Lieutenant Darius N. Couch.

Diagnosis.—This subspecies is characterized by solid body-blotches that are black anteriorly and brown posteriorly, anterior dorsal interspaces six or more scales in length, and the absence of dark stripes or rows of spots on the anterior part of the body. There are 215 to 235 ventrals, 52 to 68 caudals, and 21 to 31 dorsal body-blotches. The position of the lateral intercalary spots and lateral streaks are the same as in *deppei deppei*.

Variation.—Throughout the range of this subspecies the posterior body-blotches are brown and noticeably lighter than the anterior ones. Juveniles are colored like adults. Specimens from the northern part of the range (Nuevo León and Tamaulipas) have 21 to 28 (average 24.0) dorsal body-blotches and 7 to 11 (average 8.9) scales in the interspace between the first and second dorsal body-blotches, as compared with specimens from the southern part of the range (Hidalgo, Queretaro, and San Luis Potosí), which have 24 to 31 (average 27.7) dorsal body-blotches and 6 to 10 (average 7.8) scales in the first interspace. Likewise, there is a difference in the number of ventrals between the northern and southern samples; those from the north have an average of 228.8 ventrals, and those from the south have 222.0. In all of these characters the southern sample shows trends towards the southern subspecies, *deppei*, which has fewer ventrals, fewer scales in the first interspace, and more dorsal body-blotches.

Distribution.—Eastern part of the Mexican Plateau and lower leeward slopes of the Sierra Madre Oriental from Hidalgo and Queretaro northward to southeastern Coahuila.

Specimens examined.—Total of 28, as follows: *Coahuila*: Buena Vista, USNM 1522; 50 km. W of La Rosa, EHT-HMS 5374. *Hidalgo*: Ixmiquilpan, USNM 110890-1; 24 km. S of Ixmiquilpan, EHT-HMS 5373; Jacala, UMMZ 80937; 35 km. E of Pachuca, UMMZ 99552; 16 km. E of Tulancingo, KU 40357. *Nuevo León*: Ojo de Agua near Galeana, CNHM 33564-5. *Queretaro*: Cadereyta, UMMZ 99791-3. *San Luis Potosí*: Charcas, UMMZ 77256-8; San Diego, UMMZ 77254-5; 24 km. NE of San Luis Potosí, UIMNH 18711; 30 km. NE of San Luis Potosí, UIMNH 27150, 28135. *Tamaulipas*: Miquihuana, MCZ 19544-50.

Pituophis lineaticollis lineaticollis Cope, new combination

Arizona lineaticollis Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 300, 1861.

Pituophis lineaticollis, Stull, Occas. Papers Mus. Zool. Univ. Michigan, no. 250, p. 2, October 12, 1932, Bull. U. S. Natl. Mus., no. 175, p. 47, April 23, 1940.

Pituophis deppei lineaticollis, Smith, Proc. U. S. Natl. Mus., vol. 93, p. 460, 1943; Smith and Taylor, Bull. U. S. Natl. Mus., no. 187, p. 108, 1945.

Pituophis deppei brevilineata Schmidt and Shannon, Fieldiana-Zool., vol. 31, p. 79, February 20, 1947.

Type.—No type specimen is known. Cope (1861: 300 and 1887: 72) stated that the specimen was from the southern Mexican Plateau and that it was collected by Carlos Sartorius. Smith and Taylor (1945: 108 and 1950: 348) gave the type locality as Jalapa, Veracruz. Although this locality was the source of many specimens sent to the United States by Sartorius, it is not within the known range of *lineaticollis*, and therefore cannot appropriately be thought of as the type locality. In the absence of a type specimen and a justifiable type locality, I hereby designate as a neotype, University of Michigan Museum of Zoology, No. 114668. This specimen was collected 24 kilometers northwest of Ciudad Oaxaca, Oaxaca, on February 29, 1956, by William E. Duellman. It is an adult female having 229 ventrals, 67 caudals, and long black neck-stripes followed posteriorly by 23 light-centered dorsal body-blotches.

Diagnosis.—This subspecies is characterized by the presence of continuous dark paravertebral stripes on the anterior part of the body, and light-centered dorsal body-blotches and lateral intercalary spots (Pl. 45, Fig. 2). There are 229 to 258 ventrals, 54 to 72 caudals, and 23 to 45 dorsal body-blotches posterior to the neck-stripes. The young are colored like the adults.

Variation.—Specimens from the southern part of the range in Oaxaca have 229 to 245 ventrals (average 238.3); to the north on the Mexican Plateau in the state of Michoacán seven specimens have 231 to 243 (average 237.1) ventrals. In the relatively isolated mountain ranges of the Sierra del Sur in Guerrero and the Sierra de Coalcomán in southern Michoacán the ranges of variation and average numbers of ventrals are, respectively, 234 to 258 (245.8) and 236 to 246 (242.2). The longest neck-stripes are found in specimens from Oaxaca and Guerrero; nevertheless, some specimens from the Mexican Plateau in Michoacán and three of the four specimens from the Sierra de Coalcomán have neck-stripes equally long. One specimen from 40 kilometers north of Ciudad México and several from the vicinity of Tancítaro, Michoacán, have rather shorter neck-stripes. One specimen from Dos Aguas, Michoacán, has the neck-stripes partially fragmented into rows of spots as in *gibsoni.*

On the basis of specimens from Tancítaro, Michoacán, Schmidt and Shannon (1947: 79) described the subspecies *brevilineata,* which they diagnosed as differing from *lineaticollis* in having fewer ventrals and shorter neck-stripes. The present data suggest that the characters used to diagnose the subspecies are variable not only in Michoacán, but throughout the range of the species. Consequently, *Pituophis* (*deppei*) *brevilineata* Schmidt and Shannon (1947) is placed in the synonymy of *Pituophis lineaticollis lineaticollis* Cope (1861).

Distribution.—The southern part of the Mexican Plateau in the states of Michoacán, México, and Morelos, the Sierra de Coalcomán in southern Michoacán, and the Sierra del Sur in Guerrero and Oaxaca.

Specimens examined.—Total of 25, as follows: *Guerrero*: Acahuizotla, USNM 46537; Chilpancingo, CNHM 38356-9, UIMNH 35000, UMMZ 85724-5; Omiltemi, USNM 46462. *México*: 40 km. N of Ciudad México, UIMNH 36223. *Michoacán*: Acuaro de las Lleguas, UMMZ 112565; Dos Aguas, UMMZ 118786, 119567-8; 40 km. E of Morelia, UMMZ 101932; Tancítaro, CNHM 37126, 39069-72. *Morelos*: 1 km. W of Tepoztlán, UMMZ 101931; Tres Cumbres, UIMNH 35001. *Oaxaca*: 25 km. N of El Soledad, UIMNH 6210; 24 km. NW of Oaxaca, UMMZ 114668; San Pedro Quiechapa, USNM 110893.

Pituophis lineaticollis gibsoni Stuart, new combination

Pituophis deppei gibsoni Stuart, Proc. Biol. Soc. Washington, vol. 67, p. 172, August 5, 1954.

Type.—University of Michigan Museum of Zoology No. 107060, obtained by Colvin Gibson. Type locality: Yepocapa, Chimaltenango, Guatemala.

Diagnosis.—This race is characterized by paired, elongated, pale-centered, paravertebral spots on the anterior part of the body. Posterior to the paired spots are 22 to 27 dorsal body-blotches; these and the lateral intercalary spots have pale centers. There are 234 to 246 ventrals and 57 to 65 caudals.

Variation.—The few specimens that are available from a small geographic area do not permit a discussion of geographic variation at this time. All of the specimens have the paired paravertebral spots and blotches with light centers. In this respect the population of *lineaticollis* east of the Isthmus of Tehuantepec is noticeably different from the nominal subspecies in the Mexican highlands. Smith and Taylor (1945: 108) listed a specimen from San Cristobal, Chiapas. I have not seen this specimen and so do not know to which subspecies it belongs. On geographical grounds it probably is *gibsoni.*

Distribution.—Guatemalan highlands and probably highlands of Chipas. Aside from the specimens examined, two others are known—one from Volcán Agua, Sacatepequez (Slevin, 1939: 400), and one from Dueñas, Sacatepequez (Boulenger, 1894: 65); these localities are not shown in figure 1.

Specimens examined.—Eight, as follows: Guatemala: *Chimaltenango*: Chichavac, CNHM 1927; Finca El Tesoro, 3 km. SE of Acatenango, UMMZ 107062-3; Finca Recreo, 4.5 km. SW of Yepocapa, UMMZ 107381; Río Los Positos, 5.5 km. NE of Yepocapa, UMMZ 107061; Río Sobolopop, 8 km. W of Patzún, UMMZ 107064; Yepocapa, UMMZ 107060. *El Quiche*: Nebaj, UMMZ 89202.

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Transmitted February 2, 1960.

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28-2493

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New systematic names are in **boldface** type

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
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